

FIELD AND GARDEN STUDIES IN CROTALARIA SAGITTALIS L.  
AND RELATED SPECIES<sup>1</sup>

Donald R. Windler<sup>2</sup>

Crotalaria is a large genus of tropical, subtropical, and temperate plants comprised of about 550 species, over 400 of which occur in Africa. In 1939 Senn reported 31 species for North America with the majority growing in Mexico and the West Indies; only 21 of these species were considered to be native. Eight of Senn's 21 native species, including the Linnean C. sagittalis, form a group that is so distinctive that Rafinesque (1837) separated it into the subgenus Iocaulon.<sup>3</sup> The Iocaulon Crotalaris are annual or perennial plants characterized by simple leaves; decurrent stipules, when present; terminal or leafed-opposed inflorescences; and glabrous, inflated fruits that become black at maturity.

Polhill (1968), while dealing primarily with the African species of Crotalaria, presented a discussion of the history of generic subdivisions, discussed typification of the genus, and proposed a new arrangement of species into sections based on combinations of flower characters. The characters used were: (1) type and position of standard appendages, (2) twisting of the keel, (3) lobing of the calyx, (4) calyx-keel length ratio, (5) pubescence of the style, (6) style shape, and (7) receptacle size. Polhill placed C. sagittalis and its relatives in section Calycinae Wight & Arnott. All the characters that Polhill used for this placement were found to be consistently present in the Iocaulon Crotalaris studied.

- 
- 1 A portion of a dissertation submitted as partial fulfillment of the requirements for the Doctor of Philosophy Degree in the Department of Botany, University of North Carolina at Chapel Hill.
  - 2 Contribution number 8 from Towson State College Herbarium.
  - 3 The name Iocaulon will be used as an adjective throughout this paper to refer to the unifoliolate Crotalaris related to C. sagittalis.

During the preparation of a systematic treatment of the North American *Iocaulon Crotalarias*, extensive field collections were made in the United States and Mexico. After return to the University of North Carolina, a common garden planting was made to establish a base for the evaluation of variation patterns observed in the field. The following treatment sets forth much of the information gathered in these field and garden studies.

A publication of my revision of The North American *Iocaulon Crotalarias* should follow within the next year. New names and combinations which appear in the text have been published in Phytologia (Windler, 1971).

Topics discussed in the following presentation include: habitats, soils, garden plot data, phenology, pollination, life history, morphology, variation studies, and comments on species relationships.

#### HABITATS AND SOILS

##### Habitats

Most *Iocaulon Crotalaria* plants collected grew in dry or well drained sites in open woods or treeless areas. *Crotalaria bupleurifolia* occurs on steep, moist, north-facing slopes and appears to be the only species restricted to a shaded habitat. Though most plants of the remaining species grow in open sunlight, occasional plants were collected in varying degrees of shade. This shading resulted in plants with longer internodes and larger, less succulent leaves.

*Crotalaria sagittalis*, which is the most wide-ranging species, also varies the most in habitat and is allopatric over much of its United States range. In the gulf coastal states, however, it occasionally occurs with *C. purshii* or *C. rotundifolia* or both. In the southern and southeastern United States *C. sagittalis* grows in open pine woods, but in the midwest the plants are found on prairies, sand deposits, and waste places. In Mexico the species grows in dry, open, thorn vegetation, pine-oak or pine woods, grazing lands, south-facing slopes, and road embankments. In Mexico *C. sagittalis* is occasionally collected with other species of *Crotalaria*, most frequently *C. rotundifolia* var. *vulgaris*

which also grows well under dry conditions. Under the driest conditions plants of both C. sagittalis and C. rotundifolia fail to grow to normal size, but do produce flowers and small fruits on short peduncles. These diminutive plants frequently do not develop the narrower leaves which plants growing under favorable conditions bear at maturity and were recognized formally by Senn (1939) as C. sagittalis var. blumeriana.

Crotalaria rotundifolia and C. purshii, as mentioned above, are able to grow under the same conditions as C. sagittalis in a part of the C. sagittalis range in southeastern Louisiana and southern Mississippi. In the Atlantic coastal states, however, C. sagittalis is restricted primarily to the piedmont and lower mountains and C. rotundifolia var. vulgaris and C. purshii are restricted to the coastal plain, where they occasionally occur together. Both C. purshii and C. rotundifolia flourish in the southeastern long-leaf pine-wire grass association where C. purshii frequently is held erect by the stiff culms and blades of the wire grass and C. rotundifolia grows in the open spaces between the clumps of wire grass. Crotalaria purshii is also occasionally found growing on sandhills and savannahs.

In peninsular Florida Crotalaria rotundifolia var. rotundifolia occurs in scrub woods, in open pine stands, on sand ridges, and on road embankments. The narrow leaved C. rotundifolia from southern Florida grows primarily in basic soils on limestone similar to the soils found in the Keys.

Crotalaria polyphylla is usually collected on open pine slopes at high elevations in the mountains of western Mexico. At one locality, at an elevation of 8,000 feet (W&W 2849), the plants were growing on a grassy flat ridge in association with several species of small pines and Arctostaphylos pungens.

Crotalaria quercetorum usually occurs in dry habitats, frequently in stands of broad, coriaceous-leaved oaks or in mixed stands of the oak and species of pine. Crotalaria quercetorum occasionally grows in association with C. sagittalis in western and southern Mexico and appears to hybridize with it.

Crotalaria nayaritensis grows in both shaded and unshaded areas where moisture is available and is often found growing in close association with other plants. In such cases the diffuse

branches of C. nayaritensis intermingle with the other plants, making it difficult to locate when not in flower or mature fruit.

As was indicated above, Crotalaria bupleurifolia is the only species which is found consistently in shaded, moist conditions. Like C. nayaritensis, it grows with its branches intertwined with plants of other species making it difficult to locate and collect. Crotalaria sagittalis has been collected on dry sites near C. bupleurifolia collecting locations, but no evidence was found that any hybridization is occurring between the two species.

Since no personal collections have been made of Crotalaria pilosa, C. stipularia, C. brevipedunculata, C. mexicana, or C. nitens during this study, only notes of other collectors can be reported. Crotalaria pilosa and C. stipularia inhabit dry locations similar to those occupied by C. sagittalis, but these two species occur in the West Indies and Central and South America. Crotalaria nitens also occupies dry habitats and occurs in southern Mexico, Central America, and South America. Crotalaria mexicana and C. brevipedunculata are each known from only a few Mexican collections. Label data indicate that C. mexicana is a species of dry slopes and C. brevipedunculata is found on shaded canyon slopes.

#### Soils

At locations where field collections of Crotalaria were made, soil samples were taken. Each sample was composed of equal amounts of soil taken from around the roots of three plants. The sample was mixed thoroughly and sent to the Soil Testing Division of the North Carolina Department of Agriculture in Raleigh for testing. All samples were rated for texture and pH was tested by immersing a glass electrode in a 1:1 soil-distilled water suspension.

The information obtained for pH is summarized in Table 1. For species which occur in both the United States and Mexico, the data are presented separately for populations in each country. For the most part, the pH for the collection sites for all the species was similar. In the United States, the soil at the majority of collection locations falls between pH 5.0 and 5.9, whereas most of the Mexican material was collected from soils with the pH ranging from 6.0 to 6.9. A narrow leaved form, previously recognized by Senn as variety linaria of Crotalaria maritima, (here included in C. rotundifolia var. rotundifolia)

TABLE 1  
SOIL pH VALUES FOR Crotalaria COLLECTION LOCATIONS

Species	Range of pH					Total number of collection locations sampled
	4.5-4.9	5.0-5.9	6.0-6.9	7.0-7.9	8.0-8.5	
<u>Crotalaria purshii</u>	4	25				29
<u>Crotalaria sagittalis</u> U.S.	4	15	3			22
<u>Crotalaria sagittalis</u> MEX.		2	18	5		25
<u>Crotalaria rotundifolia</u> var. <u>vulgaris</u> U.S.	1	33	5	2		41
<u>Crotalaria rotundifolia</u> var. <u>vulgaris</u> MEX.		2	5			7
<u>Crotalaria polyphylla</u>		2	1			3
<u>Crotalaria quercetorum</u>		1	1			2
<u>Crotalaria nayarensis</u>		1	2			3
<u>Crotalaria bupleurifolia</u>			3			3
<u>Crotalaria rotundifolia</u> var. <u>rotundifolia</u>		10	8	5	3	26
TOTALS	9	91	46	12	3	161

grows on marl on the Florida Keys and on the Gulf coastal islands in soils with the pH ranging from 7.0 to 8.5. Broader leaved plants of C. rotundifolia var. rotundifolia and C. rotundifolia var. vulgaris also were found growing in circum-neutral or basic soils in Florida where the two varieties tend to intergrade. Crotalaria purshii seems to be more restricted to soils with a low pH than the other species. Twenty-seven of the twenty-nine C. purshii population soil samples had a pH falling between 4.5 and 5.4 with twenty-three ranging between pH 5.0 and 5.4.

Soil texture for all samples was reported by the Soil Testing Service as sand, loamy sand, or sandy clay loam.

#### GARDEN STUDIES

In an effort to determine what proportion of the morphological variation observed in the field was induced by variation in environmental conditions, seedlings from widely scattered locations (Table 2) representing as many parental morphological forms as possible were planted in a random sequence in a uniform garden plot at the North Carolina Botanical Garden. The seedlings were placed in holes along the center of 100-foot strips of black plastic mulching at intervals of 18 inches. Weeds between the strips were cut regularly with an 18 inch rotary mower. Temperature and rainfall statistics for the period of the study are presented in Figure 1. The plot was watered with a sprinkling irrigation system when rainfall was deficient. Soil in the garden plot was tested by the North Carolina State Department of Agriculture Soil Testing Division in Raleigh, and the ranges of test results of four samples, one from each quarter of the plot, are shown below.

Test	Range of 4 Samples
pH	5.8-6.1
Organic matter	1.3-1.7%
Calcium	456-560 ppm
Phosphorus	36-60 ppm
Potassium	56-96 ppm
Magnesium	53.6-74 ppm
Manganese	19.2-24.4 ppm

TABLE 2

LIST OF Crotalaria SEED SOURCES USED IN  
NORTH CAROLINA BOTANICAL GARDEN PLANTING.

Collection number	Locality County State	Seed parents	Plants planted	Plants harvested
1190	Scotland, North Carolina	1	20	13
2350	Monroe, Florida	2		
			21	14
2351	Monroe, Florida	1		
2358	Monroe, Florida	1	26	21
2366	Collier, Florida	6	18	18
2367	Collier, Florida	2	20	20
2372	Lee, Florida	3	21	16
2375	Pinellas, Florida	1	11	11
2377	Hillsborough, Florida	6	30	28
2384	Osceola, Florida	5	20	20
2398	Clay, Florida	2	18	16
2411	Columbia, Florida	1	8	8
2415	Suwannee, Florida	1	8	8
2421	Taylor, Florida	6	18	18
2631	Calcasieu, Louisiana	6	18	16
2645	West Feliciana, Louisiana	2	20	19
2650	St. Tammany, Louisiana	6	18	18
2659	Forrest, Mississippi	4	20	18
2668	Harrison, Mississippi	6	18	12
2669	Harrison, Mississippi	5	20	19
2672	Jackson, Mississippi	6	18	17
2697	Santa Rosa, Florida	3	18	15
2704	Walton, Florida	6	18	18
2706	Walton, Florida	5	20	19
2712	Jackson, Florida	1		
			18	13
2723	Bay, Florida	2		
2718	Leon, Florida	2	18	18
2730	Leon, Florida	6	18	18
2752	Ware, Georgia	4	20	18
2756	Glynn, Georgia	6	18	18
2762	Bulloch, Georgia	6	18	16
2768	Beaufort, South Carolina	6	18	15
2772	Barnwell, South Carolina	5	20	20
2777	Kankakee, Illinois	1	9	9
2780	Iowa, Iowa	6	18	18
2846	Cullman, Alabama	6	18	18
2848	Cherokee, South Carolina	6	18	17

TABLE 2. (Continued)

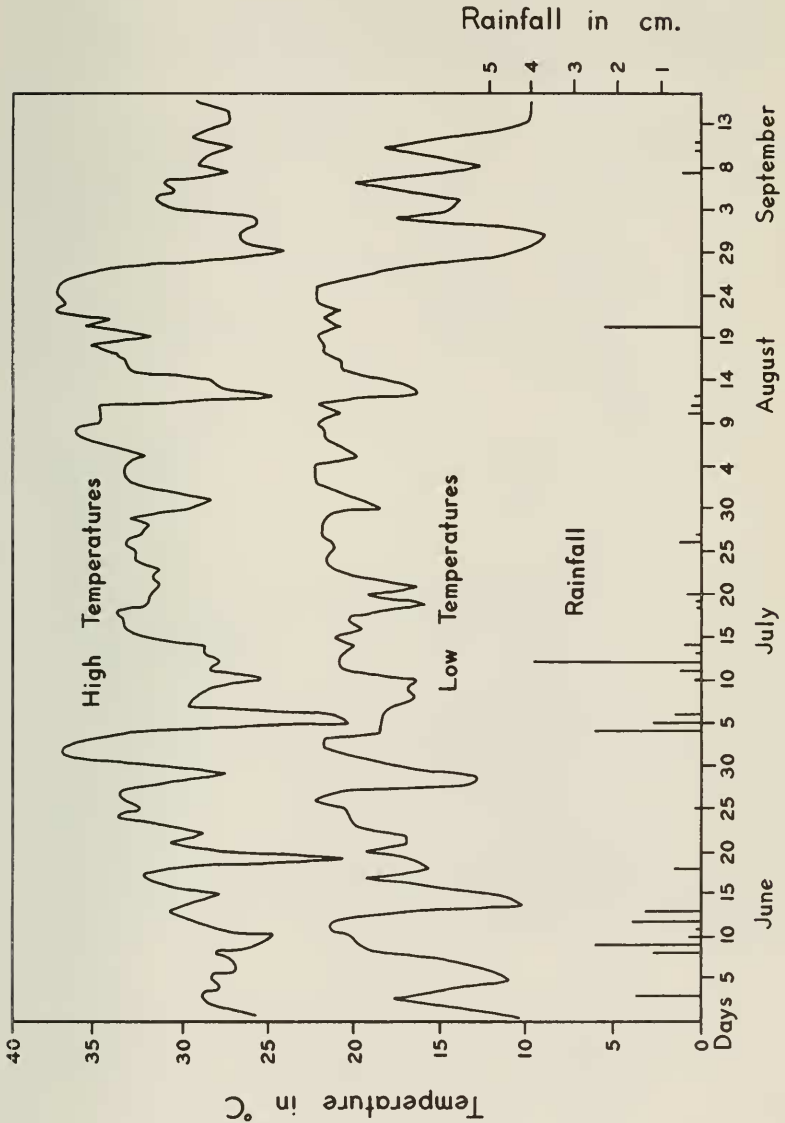
Collection Number	Locality State      Country	Seed parents	Plants planted	Plants harvested
2849	Durango, Mexico	9	32	32
2857	Durango, Mexico	2	12	12
2860	Durango, Mexico	1	5	4
2891	Nayarit, Mexico	6	18	17
2897	Nayarit, Mexico	3	19	18
2900	Nayarit, Mexico	5	20	20
2902	Nayarit, Mexico	5	22	22
2917	Nayarit, Mexico	5	18	18
2928	Jalisco, Mexico	5	20	19
2937	Jalisco, Mexico	1	7	7
2944	Jalisco, Mexico	6	19	19
2950	Jalisco, Mexico	6	27	27
2952	Jalisco, Mexico	6	19	19
2954	Jalisco, Mexico	3	15	15
2956	Jalisco, Mexico	6	20	20
2961	Michoacan, Mexico	2	15	15
2966	Michoacan, Mexico	6	18	18
2968	Michoacan, Mexico	5	29	29
2981	Oaxaca, Mexico	5	20	20
2994	Chiapas, Mexico	6	18	16
2996	Veracruz, Mexico	6	18	18
3008	Guanajuato, Mexico	3	10	8
3017	Guanajuato, Mexico	6	18	16
3035	Morelos, Mexico	6	18	18

## Seed obtained from other collections:

Irwin				
1050	Guyana	1	18	17
Stimson				
2096	Broward County, Florida	1	16	14
Stimson				
4264	Puerto Rico	1	20	20



Figure 1. Weather data for Chapel Hill, North Carolina for the period June 1, 1968-September 15, 1968.



Garden plants were harvested during the second week of September, at which time representative branches of each of the plants were pressed and dried. At the time of pressing, stem length, stem number, and plant habit data were taken for each plant. Each of the dried sets of garden specimens was compared with the dried field collections of the same number, including the seed parents of the garden plants. The following plant characters were examined in each set of specimens.

- |                      |                         |
|----------------------|-------------------------|
| I. Habit             | C. Width                |
| II. Root             | D. Pubescence           |
| A. Type              | 1. Abaxial surface      |
| B. Thickness         | 2. Adaxial surface      |
| III. Stem            | E. Petiole length       |
| A. Number            | VI. Peduncle            |
| B. Length            | A. Origin               |
| C. Maximum diameter  | B. Length               |
| D. Longest internode | VII. Bract              |
| E. Pubescence        | A. Petiolate or sessile |
| 1. Type              | B. Size                 |
| 2. Length            | VIII. Pedicel length    |
| IV. Stipule          | IX. Flower              |
| A. Width             | A. Calyx                |
| B. Lobe type         | 1. Total length         |
| C. Lobe length       | 2. Tube length          |
| V. Leaves            | 3. Pubescence           |
| A. Shape             | B. Bracteole size       |
| B. Length            | C. Corolla length       |

Table 3 shows a comparison of stem lengths between field parents and garden plants. Stem length was usually longer and ultimate leaf size was a little smaller in the garden plants than in the field parents. Of the large number of collections represented in the randomized plot, only a few plants showed a reduced size when compared with their field grown parents. Most plants of *Crotalaria rotundifolia* var. *rotundifolia* from the Florida Keys were dwarfed and some of them died. This might be attributed to a possible high soil pH or calcium requirement which is found in soil of the Keys but not in the garden soil. Plants of one collection of *C. purshii* (W&W 1190) from North Carolina were also dwarfed in the garden and this may also be attributed to soil factors. Most *C. purshii* field locations have a soil pH of only 4.5-5.4, whereas the garden soils ranged from pH 5.8-6.1.

TABLE 3 .

STEM LENGTH (IN DM.) IN FIELD AND GARDEN  
GROWN Crotalaria PLANTS

Species and Number	Field Range	Garden Range
<u>Crotalaria nayaritensis</u>		
2897	6.1-12.0	4.5- 8.0
2902	5.8- 9.0	3.9-10.5
<u>Crotalaria polyphylla</u>		
2849	1.5-3.0	2.5-5.1
2857	1.0-2.0	2.1-4.1
2860	1.0-1.8	2.3-3.7
<u>Crotalaria purshii</u>		
1190	2.6-4.5	1.2-3.1
2668	1.5-3.6	1.3-3.5
2704	up to 3.0	2.6-5.3
2752	2.5-2.8	3.1-6.8
2772	4.0-5.0	2.5-5.0
<u>Crotalaria quercetorum</u>		
2917	1.5-3.6	3.5-6.4
2928	1.5-3.3	2.8-4.5
<u>Crotalaria rotundifolia</u> var. <u>rotundifolia</u>		
2350	2.5-6.5	1.1-3.5
2351	3.5-6.0	1.4-1.9
2358	1.0-2.0	1.3-4.6
2366	1.5-3.0	2.0-5.4
2367	1.5-2.3	2.0-4.4
2372	1.0-1.8	2.5-4.5
2375	1.2-1.9	1.8-4.1
2377	1.5-2.2	2.8-5.5
2384	1.5-2.8	2.0-4.4
2398	1.0-1.5	2.0-5.5
2421	1.0-1.2	3.3-6.3
2672	1.5-2.0	3.5-4.8
2756	1.0-2.0	2.5-3.5

TABLE 3. (Continued)

Species and Number	Field Range	Garden Range
<u>Crotalaria rotundifolia</u> var. <u>vulgaris</u>		
2411	1.0-1.5	2.8-4.0
2415	1.0-1.2	3.5-4.8
2645	1.0-2.0	2.8-5.0
2650	1.2-3.7	1.3-5.3
2669	1.2-2.5	2.8-5.3
2706	1.0-2.2	1.9-4.5
2730	2.4-2.5	2.5-6.0
2762	1.3-3.2	2.3-5.5
2768	3.4-3.5	1.8-4.5
2900	1.0-2.8	4.5-8.1
2952	0.4-5.0	3.6-7.3
3017	0.5-1.5	1.1-2.4
3035	0.5-1.0	3.3-6.3
<u>Crotalaria sagittalis</u>		
2631	1.5-2.8	3.8-6.5
2777	1.5-3.7	3.8-6.0
2780	1.5-2.1	3.0-6.3
2846	1.0-2.5	2.5-4.3
2848	3.4	3.0-5.3
2891	1.3-5.0	4.8-6.6
2944	1.7-4.5	2.4-6.8
2950	0.3-1.8	2.0-4.8
2954	1.3-3.2	2.8-5.1
2956	0.3-1.6	3.0-7.6
2961	1.2-4.5	3.3-4.8
2966	0.5-1.5	2.8-4.6
2968	0.6-2.5	4.1-8.3
2981	0.3-1.2	3.5-7.1
2996	1.5-5.5	3.2-6.6
3008	0.5-1.4	3.0-5.6
<u>Crotalaria stipularia</u>		
Irwin 1050	1 plant - 1.5	2.0-5.3
Stimson 4264	1 plant - 2.8	6.5-9.0

Comparisons of several field collections which showed a great variation in leaf size and shape with their garden progeny showed equal variation to be maintained in the garden. In several of these cases the relatively few (usually three to six) offspring of a single plant exhibited nearly the full range of leaf variation that appeared in an entire field collection.

Though many of the garden plants grew to be larger than their field counterparts (Table 3), most of them had a habit very similar to that of the plants from the field collections. Plants of Crotalaria sagittalis from United States locations were exceptions to this. In this species young garden plants had a habit much like that seen in the field, but as the plants grew older, they assumed an uncharacteristic sprawling habit.

Seeds were planted from a number of representative plants of Crotalaria sagittalis var. blumeriana, a taxon characterized by small plant and fruit size. All of the resulting garden plants were as large as any of the plants grown from field seed of typical Mexican C. sagittalis. Due to consistent results of this type for all of the C. sagittalis var. blumeriana seed planted, I do not recognize the variety taxonomically. The garden plants grown from C. sagittalis seed from locations 2954, 2961, and 2966 in Mexico had a habit unlike any seen in the field. The garden habit was like that of a small, dense, flat-topped bush. Although the garden material of these three collections is quite distinct from other C. sagittalis grown in the garden, it seems necessary to include this entity under C. sagittalis since its field parents fall within the range of variation found in other C. sagittalis field collections. Further study may show these "garden taxa" to be good species.

#### PHENOLOGY

Under good growing conditions plants of most species of Iocalon Crotalarias seem to be day neutral. Once flowering has begun it usually continues until growth is halted by either drought or cold weather.

Crotalaria plants grown in the experimental plot from places as far from each other as Chiapas, Mexico and Northern Illinois flowered under the same day length conditions in Chapel Hill. Plants of Crotalaria nayaritensis, the Mexican species which grew to the largest size of any of the garden plantings,

did not flower until late in the growing season and then flowered only sparingly. The fact that flowering occurred as the days were getting shorter may reflect a requirement of C. nayaritensis for relatively short days prior to flowering.

#### POLLINATION

Early in the studies, during growth chamber work with Crotalaria sagittalis and C. purshii, fruit set occurred on all plants observed in the absence of pollinators. This seems to indicate that a mechanism for self-pollination is operative in the group. To check how extensively automatic self-pollination occurs in the species studied, inflorescences of a number of garden plants (Table 4) of each of seven taxa were caged, using white nylon stockings over a frame formed by half gallon waxed milk cartons with the sides cut out. All open flowers and fruits were removed from inflorescences before the cages were put in place and the nylon netting was tied below the inflorescences. In most cases two inflorescences were enclosed within each cage.

Results from the caging (Table 4) show that in the absence of insects, some of the plants set fruit while others did not. These results may be explained in several ways. Some of the plants may have been self-sterile and even though the pollen of the flower reached the associated pistil, no fruit was set. Under these conditions, a low fruit set might be expected in uncaged plants if very few individuals of the species were present in the garden to serve as pollen sources. This may have been the case in the plants of Crotalaria nayaritensis and C. polyphylla (Table 4). Plants of C. rotundifolia var. rotundifolia from the United States and C. rotundifolia var. vulgaris from Mexico showed mixed results. In variety rotundifolia representatives of one population selfed in five of the five cages, but in five plants from three other locations no fruit set occurred. Similarly, in Mexican variety vulgaris two plants from one population failed to set fruit, while three plants from two other populations did set fruit. All uncaged representatives of Mexican C. rotundifolia var. vulgaris set fruit abundantly as shown by the average fruit per plant range of 23-136. Since numerous C. rotundifolia individuals were present to act as a source of pollen for the pollen vectors, high fruit set might be expected even though some of the populations appeared to consist of self-sterile plants.

TABLE 4  
FRUIT SET INFORMATION FOR GARDEN GROWN Crotalaria PLANTS  
WITH CAGED INFLORESCENCES AND AVERAGE FRUITS PER PLANT IN UNCAGED PLANTS

Country and Species	Collection Number	Number of branches caged (1-3 inflorescences per cage)	Number of branches of fruit setting	Average fruit per plant (for all uncaged plants)
MEXICO				
<u>C. nayaritensis</u>	2902	5	0	0.3
<u>C. polyphylla</u>	2849	5	0	0.8
<u>C. sagittalis</u>	2966	5	5	14.2
<u>C. rotundifolia</u>	2900	2	0	57.1
var. <u>vulgaris</u>	3035	2	2	136.2
	2952	1	1	22.8
PUERTO RICO				
<u>C. stipularia</u>	Stimson 4264	5	5	131.7
UNITED STATES				
<u>C. sagittalis</u>	2631	2	2	41.3
	2780	2	2	231.0
	2846	1	1	91.3
	1190	2	2	4.8
<u>C. purshii</u>	2752	2	2	4.0
	2772	1	1	5.4

TABLE 4. (Continued)

Country and Species	Collection Number	Number of branches caged (1-3 inflorescences per cage)	Number of branches setting fruit	Average fruit per plant (for all uncaged plants)
<i>C. rotundifolia</i> <u>var. rotundifolia</u>	2372	5	5	8.3
	2384	2	0	39.8
	2398	2	0	25.6
<i>C. rotundifolia</i> <u>var. vulgaris</u>	2672	1	0	55.0
	2718	2	2	26.9
	2730	4	4	33.1
	2762	1	1	42.9
	2768	1	1	38.5



Another possible explanation for the results would involve a system in which insect movement of the flower parts would be necessary for self-pollination to occur. This does not appear to be the case in garden plants of Crotalaria polyphylla, which flowered profusely, had insects visiting the flowers, but still very little fruit set. It could, however, be the situation in some populations of C. rotundifolia in which uncaged plants set fruit abundantly, but caged plants set no fruit. Such a system would also bring foreign pollen to flowers and promote new variation through occasional recombination. This explanation may account for the extreme variability maintained in the Florida populations of C. rotundifolia and the Mexican populations of C. nayaritensis and C. bupleurifolia.

Continuous selfing, if occurring almost to the exclusion of all out-crossing, would tend to maintain a few genetic lines in a species and account for the occurrence of extremely homogeneous populations, like those in Crotalaria sagittalis, with local variations caused by rare out-crossing, by genetic drift, or by occasional mutation and local selection over many generations.

The actual mechanism of pollination in the American Crotalaria species is not fully understood. Polhill (1968, page 181) explains this in the following way for some of the African species:

"The genus is entomophilous and the visiting insect depresses the keel; pollen shed into the keel before the flowers fully open is extruded on the style by a piston action, which can be repeated several times (unlike the explosive release of pollen by several north-temperate genera of Genisteae)."

Whether the species for which this applies are self-fertile or self-sterile, I do not know. If the plants of a species were self-sterile, nothing in the way of a morphological change would be needed to convert the flower to a self-pollination system, since the pollen of the flower covers the stigma during the piston action.

Observations of numerous flowers of Iocaulon Crotalarias show that in most cases the carinal tube of the keel above the stigma is filled with masses of pollen grains which adhere to each other. Other flowers examined had the short anthers beside

or above the stigma in the carinal tube with pollen still remaining in the tardily dehiscent anther locules. Under usual circumstances, if pollen from another plant reaches the stigma it does so through the mass of the flower's own pollen. While examining buds for chromosome counts in the various species, occasional buds were found in which all the anthers failed to produce pollen-mother-cells or pollen. This condition would allow any pollen transported to the carinal tube by an insect vector to reach the stigma and complete pollination. A similar type of male sterility has been reported for Crotalaria striata (Kempna & Krishna, 1958). Even in the low percentages at which this male sterility seems to occur in these species, the increased potential for gene exchange caused by the mechanism is sufficient to assure that a variable gene pool will be maintained.

Even though one to three hours were spent at each field location sampled (during the period when the flowers were fully open) insects were only occasionally observed working the flowers. In addition to honey bees, several small bees were also observed and collected. They were identified by Dr. Gerald I. Stage, Assistant Curator, Division of Hemiptera and Hymenoptera, Department of Entomology, Smithsonian Institution, Washington, D. C., as sweat bees with the following classification:

Halictidae: Halictinae

Lasioglossum (Dialictus) raleighensis Crawford

Collected in Jackson County, Mississippi and  
Bacon County, Georgia.

In the garden studies in Chapel Hill, North Carolina numerous bees were observed working the flowers during the summer. Representatives of each of the observed types were also sent to Dr. Stage for his determinations:

Halictidae: Halictinae (Sweat bees)

Lasioglossum (Dialictus) sp.

Megachilidae: Megachilinae (Leaf cutter bees)

Megachile (Litomegachile) b. brevis Say

Megachile (Leptorachis) petulans Cresson

Megachile (Chelostomoides) campanulae wilmingtongi  
(Mitchell)

Anthophoridae: Xylocopini (Carpenter bees)

Xylocopa virginica virginica (Linnaeus)

Apidae: Apinae (Honey bees)

Apis mellifera Linnaeus

The bees did not appear to restrict themselves to any single species of Crotalaria, but moved from one species to another in a short period of time. One bee, which was followed for a period of time, visited 22 plants representing seven of the taxa included in the garden.

#### LIFE HISTORY, MORPHOLOGY AND VARIATION STUDIES IN Crotalaria Seeds

The seed characters of native and introduced Crotalarias known to occur in the New World have been covered quite well in a lengthy USDA Technical Bulletin (No. 1373) by Dr. Robert H. Miller, USDA Crops Research Division, Beltsville, Maryland. Six North American Iocaulon Crotalaria taxa are included: Crotalaria rotundifolia (C. maritima), C. nitens, C. pilosa, C. purshii, C. sagittalis, and C. stipularia. Miller treated C. rotundifolia var. vulgaris (Senn's C. angulata) and Senn's C. tuerckheimii as synonymous with C. sagittalis L. and treated C. rotundifolia var. rotundifolia as C. maritima Chapman.

The uniformity of the seeds in the 47 African, Asian, and New World species of Crotalaria studied anatomically was such that Miller declined to develop an anatomical key to the seeds "because of the relatively few differences in available diagnostic characters." The seed in Crotalaria sagittalis develops from a campylotropus-like ovule and is non-arillate. Detailed seed development is discussed in a paper by Cook (1924).

A hard seed coat, which is characteristic of many legumes, is also present in Crotalaria. This character, coupled with a low seed moisture content, is credited with the extreme longevity of seeds of many plants in the family. Quick (1961) reported experiments by Becquerel showing Cassia seeds to be viable after 115 and 158 years. Quick also discussed the work of Ewert in which seeds, all over 50 years old, from 1,400 species and varieties of plants were tested. Of the 1,400 samples only 49 contained viable seeds and 37 of the 49 species represented were legumes. The oldest of these 37 samples were of seeds of Goodia and Novea, both 105 years old.

Length and color data for seed collected in the field were obtained prior to garden plantings for most of the species. Seed color was checked by comparison with color plates in Maerz and Paul (1950), but proved to be too variable even in single samples to be of value as a taxonomically diagnostic tool. Seed

length, obtained by measuring the longest axis of the cotyledonary lobe, was used as an index to seed size and the resulting data from this study are presented in Table 5. Seed size reported in the tables was maintained in the garden plants grown from seed measured for the tables. Seed size, while not important as a diagnostic character is interesting in that it tends to be related to geographic distribution. This is most readily observed when comparing the figures for populations of Crotalaria sagittalis for which the greatest north-south range is available. Plants in northern Illinois and Iowa produced seed with average lengths of 2.54 mm and 2.72 mm respectively. In comparison plants of the eastern Texas population had a mean seed length of 1.85 mm. Geographically intermediate plants in Louisiana and Missouri had intermediate mean seed lengths of 2.03 mm (La.), 2.31 mm (La.), and 2.51 mm (Mo.). In Mexico, the smallest C. sagittalis seeds were collected at the lowest elevations. Collection 2891 with a mean seed length of 1.67 mm grew at 2,800 feet, whereas collections 2956, 2968, and 2970 with mean seed lengths between 2.06 and 2.09 mm grew at elevations of 5,500-6,500 feet. This general correlation between seed size and latitude in the central United States and seed size and elevation in Mexico suggests that a larger seed size may be of an adaptive advantage in cooler climates. In the United States the larger seed size may be advantageous for the northern plants because the larger supply of storage products allows the young plants to take the fullest advantage of the shorter growing seasons. In Mexico, where the growing seasons are controlled more by the fluctuations in rainfall than by temperature changes, the advantage of a larger seed size at higher elevations is not as clear. The higher elevations are definitely cooler and their growing seasons may be shorter due to reduced rainfall periods, but no information on growing season length in relation to elevation is available for the collection locations visited.

#### Seed Germination

Plants in populations of the Iocalon Crotalarias are usually well scattered and frequently limited to 10-15 per location. This small population size occurs in spite of the fact that viable seeds are normally produced in large numbers. To determine the approximate normal percentage of germination, one year old seeds from plants from seven locations were tested. The seeds were submerged in petri plates containing distilled water at room temperature during the test. Records on germination were kept for a period of two weeks. Table 6 below shows that

TABLE 5.

SEED SIZE (mm) IN FIELD COLLECTIONS OF Crotalaria SEED  
(LENGTH OF COTYLEDONARY LOBE)

Species and Number	Country and State	Sample Size	Range	Mean	Standard Deviation	Standard Error
<u>Crotalaria polyphylla</u>						
2849	MEX, Dur.	100	1.90-3.00	2.51	0.18	0.018
<u>Crotalaria purshii</u>						
2668	US, Miss.	100	1.95-2.35	2.10	0.10	0.010
2676	US, Ala.	100	1.95-2.35	2.16	0.10	0.010
2696	US, Fla.	100	2.10-2.80	2.34	0.16	0.016
2728	US, Ga.	100	1.95-2.40	2.14	0.11	0.011
2752	US, Ga.	96	2.00-2.60	2.19	0.11	0.011
2767	US, S.C.	100	1.95-2.30	2.13	0.09	0.009
2772	US, S.C.	100	2.05-2.65	2.41	0.16	0.016
<u>Crotalaria quercetorum</u>						
2928	MEX, Jal.	100	1.35-1.70	1.48	0.10	0.010
2994	MEX, Chs.	100	1.35-2.00	1.61	0.16	0.016
<u>Crotalaria rotundifolia</u> var. <u>rotundifolia</u>						
2350	US, Fla.	86	1.85-2.20	2.00	0.10	0.011
2358	US, Fla.	100	1.85-2.15	2.03	0.07	0.007
2366	US, Fla.	100	1.90-2.30	2.06	0.09	0.009
2367	US, Fla.	50	1.95-2.30	2.08	0.09	0.012
2372	US, Fla.	70	1.95-2.60	2.25	0.16	0.020
2377	US, Fla.	100	1.70-2.20	2.00	0.10	0.010
2379	US, Fla.	100	1.95-2.55	2.15	0.13	0.013
2398	US, Fla.	100	1.80-2.35	2.07	0.09	0.009
2421	US, Fla.	100	1.75-2.10	1.96	0.09	0.009
2672	US, Miss.	100	1.80-2.25	2.11	0.08	0.008
2756	US, Ga.	100	1.75-2.20	2.00	0.11	0.011

TABLE 5. (Continued)

Species and Number	Country and State	Sample Size	Range	Mean	Standard Deviation	Standard Error
<u>Crotalaria rotundifolia var. vulgaris</u>						
2645	US, La.	100	1.90-2.30	2.06	0.09	0.009
2650	US, La.	100	1.85-2.45	2.04	0.09	0.009
2669	US, Miss.	100	1.80-2.35	2.06	0.12	0.012
2706	US, Fla.	108	2.10-2.70	2.45	0.14	0.014
2718	US, Fla.	95	1.90-2.30	2.05	0.07	0.008
2730	US, Fla.	100	1.65-2.05	1.94	0.08	0.008
2740	US, Ga.	122	1.85-2.30	2.05	0.11	0.010
2742	US, Ga.	100	1.80-2.35	2.12	0.10	0.010
2762	US, Ga.	112	1.75-2.25	2.00	0.10	0.010
2768	US, S.C.	100	2.00-2.50	2.16	0.11	0.011
2900	MEX, Nay.	100	1.55-2.00	1.83	0.12	0.012
2952	MEX, Jal.	100	1.75-2.30	1.94	0.14	0.014
3035	MEX, Mor.	100	1.55-1.85	1.74	0.09	0.009
<u>Crotalaria sagittalis</u>						
2604	US, Tex.	100	1.50-2.15	1.85	0.15	0.015
2631	US, La.	100	1.55-2.30	2.03	0.10	0.010
2635	US, La.	100	2.15-2.60	2.31	0.10	0.010
2777	US, Ill.	100	2.30-2.75	2.54	0.07	0.007
2780	US, Iowa	100	2.45-3.00	2.72	0.12	0.012
2843	US, Miss.	100	2.05-2.85	2.38	0.15	0.015
2846	US, Ala.	100	2.10-2.65	2.31	0.10	0.010
2848	US, S.C.	100	2.00-2.50	2.24	0.12	0.012
2891	MEX, Nay.	100	1.45-1.95	1.67	0.14	0.014
2903	MEX, Nay.	100	1.65-1.95	1.81	0.07	0.007
2944	MEX, Jal.	100	1.65-2.10	1.81	0.07	0.007
2950	MEX, Jal.	100	1.65-2.10	1.87	0.13	0.013
2956	MEX, Jal.	90	1.50-2.35	2.06	0.12	0.012
2968	MEX, Mich.	100	1.80-2.40	2.06	0.11	0.011
2970	MEX, Oax.	100	1.90-2.40	2.09	0.13	0.013
2981	MEX, Oax.	100	1.85-2.15	1.99	0.07	0.007
2996	MEX, Ver.	100	1.70-2.10	1.96	0.08	0.008

from 0 to 11% of the seeds swelled and germinated in the untreated seed samples.

Germination studies made prior to the garden planting showed that 90-100% germination was usual in seed which had been mechanically scarified by scratching the testa with a dissecting needle. The low natural germination rates of Crotalaria seed are compatible with the low numbers of plants at most collection locations, but do not explain the large numbers of plants occasionally found at some locations. Weathering is usually credited with bringing about germination in legume seeds which have been exposed for long periods of time and alternate freezing and thawing, rains, soil chemicals, soil micro-organisms, and high summer temperatures probably do act to increase germination. In alternate freezing and thawing of submerged Crotalaria sagittalis (W&W 2780) seeds there was no increase in swelling of seeds during or after eight freeze-thaw cycles.

Martin and Cushwa (1966) reviewed the literature on the effects of high temperature on the germination of legume seeds and presented additional data from their own experiments with Cassia seed. It had been previously observed that the abundance of legumes in pine woods was increased following fires. Martin and Cushwa hypothesized that this could be accounted for by the breakdown of the seed coat by the high temperatures generated during fire. They performed experiments in which Cassia seeds were subjected to increasing temperatures under moist and dry conditions. Dry heat increased germination in new seed slightly with a maximum of 22% germination at about 90-95° C. The new Cassia seed reached a maximum germination rate of nearly 100% after being exposed to 80° C moist heat for four minutes. Exposure at 80° C for periods up to 16 minutes did not reduce the germination percentages. Martin and Cushwa indicated that they thought that these moist, hot conditions are duplicated in burning pine litter, but they have not been able to establish this experimentally.

In order to test the reaction of the Crotalaria seed to heat, two additional lots of 100 seeds were taken from the same seven collections mentioned above. One of the lots was placed in boiling water and allowed to cool to room temperature; the other lot was placed in water maintained at 82° C for a period of 20 minutes, following which it was allowed to cool.

Germination results of these tests at the end of two weeks appear in Table 6 along with the results from the untreated seed samples. In all cases seeds scalded with boiling water showed an increase in germination over untreated seeds, but in most cases the increase was not as great as that shown by seeds subjected to prolonged high temperature. It is evident from Table 6 that heating does have the effect of increasing Crotalaria seed germination, but under field conditions the degree of temperature and moisture and the duration of hot moist conditions would vary with the position of a seed in the soil during a fire. It is probable that only a small proportion of the total number of seeds present are in a position of a seed in the soil during a fire. It is probable that only a small proportion of the total number of seeds present are in a position to benefit from burning at a given time, thereby much reducing the fire induced germination percentages one might expect to receive in a field experiment.

TABLE 6.

SEED GERMINATION IN SEVEN 1 YEAR OLD  
Crotalaria SEED SAMPLES (SAMPLE SIZE 100)

Species	Population number	Untreated	Scalded	Heated 82° C/ 20 minutes
<u>C. quercetorum</u>	2917	3	73	98
<u>C. rotundifolia</u> var. <u>rotundifolia</u>	2377	2	61	93
<u>C. rotundifolia</u> var. <u>vulgaris</u>	2645	4	20	38
<u>C. rotundifolia</u> var. <u>vulgaris</u>	3035	11	22	73
<u>C. sagittalis</u>	2780	0	24	6
<u>C. sagittalis</u>	2968	0	69	86
<u>C. stipularia</u>	Stimson 4264	6	85	100



Frequently after soil disturbance, Crotalaria plants become more abundant. This may be attributed to the germination of newly exposed, weathered seeds or of seed scarified during the disturbance. The extent to which animals act as seed scarifying agents in Crotalaria is not known. Fruits examined after infection by Crotalaria Moth (Utethesia) larvae, which bore into young fruits and eat the developing seeds, occasionally contained seeds which had a small part of the seed coat and a bit of cotyledon tissue missing, thus exposing the embryo for water uptake. Seeds of this type were germinated and developed into normal seedlings without further scarification. Since seeds of Crotalaria have been known to cause Senecio illness and death in mammals and birds due to the alkaloids in the seed coat (Kingsbury 1964), the effectiveness of the digestive tract of animals in scarification of Crotalaria has not been tested during this study.

Once scarified, Crotalaria seed must come in contact with water and in most cases must remain in contact with moisture until the seedling is anchored and the cotyledons emerge. In greenhouse work, swollen seeds were usually covered by a thin layer of milled sphagnum to about the same depth as the thickness of the seed. Occasionally seeds were covered accidentally to a depth of  $\frac{1}{4}$  inch and these did not complete germination.

#### Seedling Development

Seedling development is initiated by the growth of the radicle which grows downward and becomes anchored in the soil. This stage is followed by an elongation of the hypocotyl which elevates the cotyledons. As the seed swells the testa softens and the cotyledons enlarge and split the testa which then dries and falls away. Occasionally the seed coat dries over the tips of the cotyledons and holds them together. In these cases if the cotyledons are held together over most of their length, the epicotyl fails to develop and the seedling dies.

Following the loss of the seed coat, the cotyledons, relatively equal in size, expand to their maximum size within about one week. In late spring in the greenhouse, two weeks after swollen seeds were planted, the first true leaf was fully expanded and the second present, though in a folded and unexpanded condition.

Figure 2 shows silhouettes of representative seedlings of nine of the Crotalaria taxa studied. Variation among seedlings



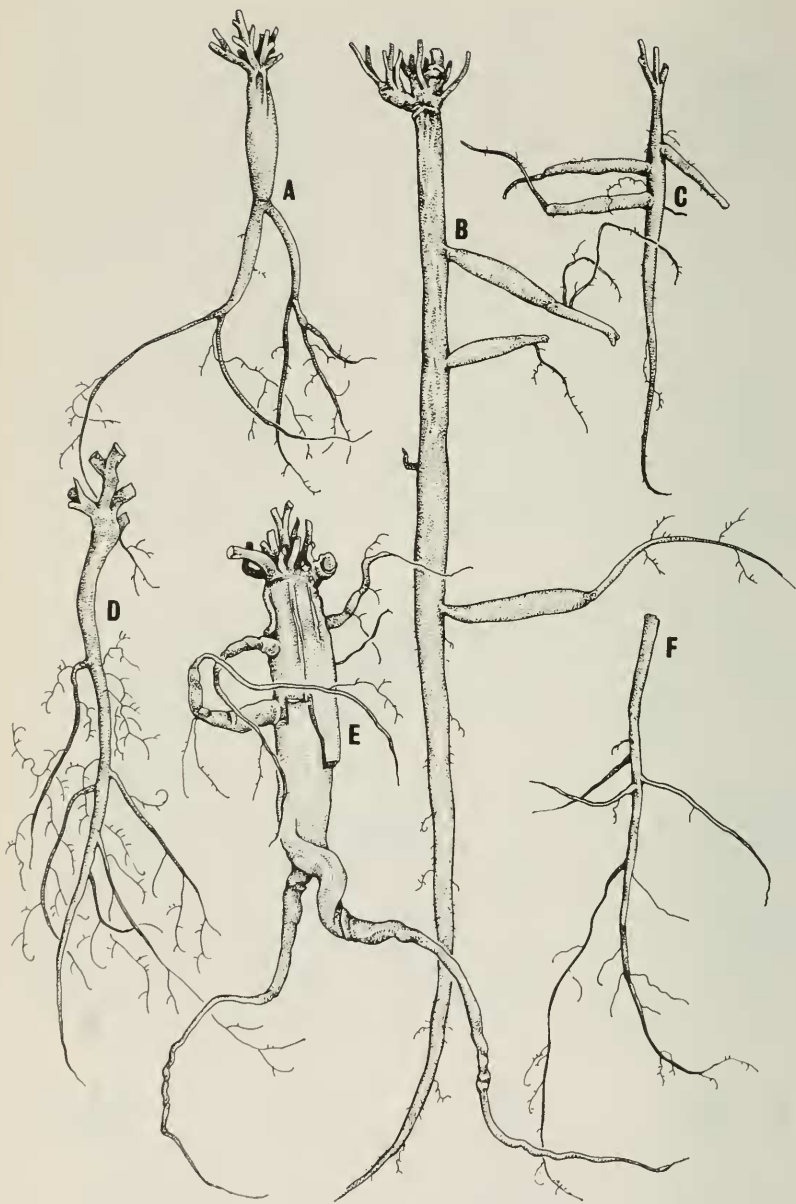
from a given population is relatively small and cotyledon size varies with the seed size. Hypocotyl length (as measured from the base of the cotyledons to ground level) varies from species to species with the hypocotyls of C. rotundifolia and C. purshii being shortest. Figures 2 A-H illustrate seedlings with short hypocotyls and the remainder (I-O) illustrate those with long hypocotyls. All seedlings were two weeks old with the exception of C and D which were four weeks old and J which was three weeks old. Seedlings C, D, and J have been included to show a comparison of the early branching exhibited by plants which later become decumbent (C and D) with the branching of those which are erect at maturity (J). In most Iocaulon Crotalaria species there is a tendency for young, rapidly growing seedlings to be erect or ascending as exemplified by C. rotundifolia from Florida (Figure 2 C). Figure 2 D shows the most common early branching form throughout the range of both varieties of C. rotundifolia. Early internodes of the main stem of C. rotundifolia are short, allowing for several decumbent branches to arise near the ground. Figure 2 J shows C. sagittalis after three weeks of growth. As is typical in the species, both the hypocotyl and internodes are long and growth is rapid. In five and one-half weeks the greenhouse grown C. sagittalis plants began flowering and in nine and one-half weeks mature black fruits were present.

#### Roots

Plants of all species of the Iocaulon Crotalarias have slender taproots (similar to Figure 3 F) when they are young. Figures 3 D and F illustrate the root growth form found in mature annual plants. Crotalaria sagittalis usually falls into this group, but in the warmer parts of its range some plants

---

Figure 2. Silhouettes of Crotalaria seedlings of various ages, 0.29x. (See text for discussion). A. C. rotundifolia var. rotundifolia (W&W 2350). B. C. rotundifolia var. rotundifolia (W&W 2398). C. C. rotundifolia var. rotundifolia (W&W 2377). D. C. rotundifolia var. rotundifolia (W&W 2398). E. C. rotundifolia var. rotundifolia (W&W 2377). F. C. purshii (W&W 2684). G. C. rotundifolia var. vulgaris (W&W 2645). H. C. rotundifolia var. vulgaris (W&W 3017). I. C. sagittalis (W&W 2777). J. C. sagittalis (W&W 2777). K. C. bupleurifolia var. robusta (Rzedowski 15,134). L. C. stipularia (Stimson 4264). M. C. nayaritensis (W&W 2902). N. C. quercetorum (W&W 2917). O. C. polyphylla (W&W 2849).



produce roots which perennate. In the perennial species, the main root axis and branches become thickened in the manner shown in Figures 3 A, B, C, and E. In cool climates the stems of the perennial species become dormant and frequently die back in the winter, and new stems are produced the following year from a crown. The number of stems produced in successive years varies from one to several in C. purshii and perennial C. sagittalis to many in C. rotundifolia. Figure 3 B illustrates the type of perennial root structure of plants growing in the deep sands of Florida. In comparison 3 E shows a root from a plant of the same species growing in less porous soils.

Root systems of all Crotalaria plants grown in the garden were much alike. None of the garden plants produced the long tap roots typical of those found in the field; all produced roots in which the main axis was regularly short and had numerous relatively thick branches near the surface. The near-surface roots possibly developed in response to the high soil moisture in the upper several inches of soil under the plastic mulching.

Very little has been published on the anatomy of roots of the Locaulon species of Crotalaria. Britton (1903) published a brief description and a drawing of a secondary root cross section of C. sagittalis, and pointed out the abundance of sclerenchyma cells in the cortex. He also stated that the roots closely resembled those of Cassia except for having a greater abundance of the cortical sclerenchyma tissue. Hand sections of C. sagittalis roots observed by the author were similar in structure to those illustrated by Britton. No attempt was made to survey the anatomy of the roots of other species.

Roots of Crotalaria produce nodules, but no effort was made to determine what percentage of the plants obtained in the field possessed nodules or the associated bacteria. A study

---

Figure 3. Representative roots of Crotalaria species, ca. 0.5x. A. C. rotundifolia var. rotundifolia (W 1142). B. C. rotundifolia var. rotundifolia (W&W 2383). C. C. purshii (W 1072). D. C. nayaritensis (W&W 2897). E. C. rotundifolia var. rotundifolia (W&W 2736). F. C. sagittalis (W&W 2777).

of root nodule organisms in wild legumes by Conklin (1936) included organisms which were associated with the roots of C. sagittalis. Results from Conklin's cross inoculation studies showed a strong similarity between the organism which is associated with C. sagittalis and those associated with Vigna sinensis, Genista tinctoria, and Baptisia tinctoria. A later study by Wilson (1944) reported that isolates from 33 genera entered into symbiosis with C. sagittalis. During the present study well developed nodules were observed on roots of eight week old C. sagittalis plants grown in the greenhouse.

#### Trichomes

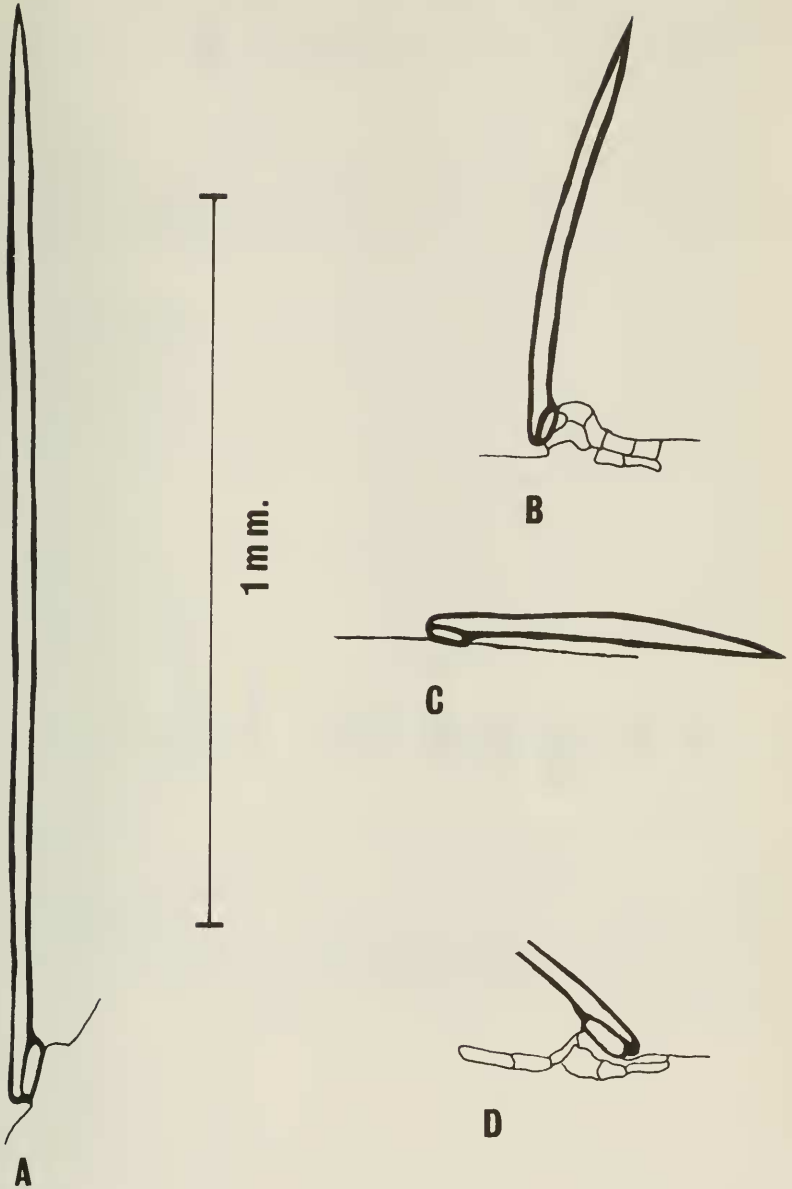
Most above-ground organs except the fruits and stamens of the Iocaulon Crotalarias are pubescent to some degree. Even the yellow banner may bear some trichomes on the back and at the base. Leaves usually bear trichomes on both surfaces and on the margin, but in Crotalaria purshii and C. quercetorum the upper surfaces are glabrous, and the trichomes are restricted to the lower surface and margins.

Organs vary in trichome density, and the trichomes vary in length, but the trichome type is consistent in all taxa of the Iocaulon Crotalarias studied. The trichomes are non-glandular and consist of a long terminal cell attached laterally at the base to a small cell which is in turn attached to the epidermal cells. The angle which the trichome takes relative to the organ surface is determined by the structure of the epidermis at the point of the attachment (Figure 4). If the attachment is to a flat surface (Figure 4 C), the trichome is strongly appressed, but if the surface is papillate and the attachment is on the side of a papilla of epidermal cells (Figure 4 B) the trichome is spreading. Intermediate angles depend on the size of the papilla and the angle of basal cell attachment to the papilla (Figure 4 A and D).

The trichomes discussed above closely resemble one of the trichome types which Metcalfe and Chalk (1950) illustrate as

---

Figure 4. General trichome types in Iocaulon Crotalarias illustrating the various forms of attachment in relation to the axis of the stem (or surface of leaf, etc.). A., D. Intermediates between appressed and spreading trichomes. B. Spreading trichome. C. Appressed trichome.



ordinary papilionaceous hairs. All of the trichome types which they place into this group are terminated by a long pointed cell, but differ from one another in the number and relative length of basal cells and their attachment to the terminal cell.

#### Stipules

The foliaceous decurrent stipules which wing the stems of members of the Iocaulon Crotalarias are quite unique. Linnaeus considered the stipules to be so important that he placed all of the Iocaulon species collectively into a single species with the epithet "sagittalis" a term previously used by Plukenet and Hermann to describe the stipules.

Of the 12 North American Iocaulon species of Crotalaria I recognize, plants of four species lack stipules completely. In several of the remaining species, however, stipules are of such diagnostic importance that stipule type alone is enough to identify a plant to species. For example, the incurved stipule lobes in plants of C. stipularia (Figure 5 A) are not approached in form in any other species and furnish adequate identification of this taxon. The most common stipule type in the group is that in which the lobes are spreading (Figure 5 B, C, D, E, F, and H). Stipules in C. bupleurifolia var. bupleurifolia are usually quite distinct because they are wider than the stipules of other species and do not tend to taper to the base (Figure 5 G). Stipules in C. pilosa, which was not collected during the study, also tend to be parallel to the stem, but are usually quite narrow, rarely having spreading lobes, and always being decurrent for more than one internode.

The silhouettes in Figure 5 illustrate the stipule variation in the various taxa of Iocaulon Crotalarias. Stipules were included from wide and narrow leaved plants for species where

---

Figure 5. Silhouettes of decurrent stipules of Crotalaria species; A-F, 0.13x; G-H, 0.15x. A. C. stipularia. B. C. purshii. C. C. sagittalis, five on left from Mexican collection, remainder from United States collections. D. C. rotundifolia var. rotundifolia. E. C. rotundifolia var. vulgaris, United States collections. F. C. rotundifolia var. vulgaris, Mexican collections. G. C. bupleurifolia var. bupleurifolia. H. C. nayaritensis.

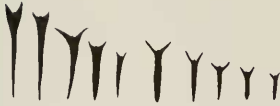




A



B



C



D



E



F



G



H

this variation occurs. Stipule size does not vary with the leaf width in the material examined; some of the plants in C. sagittalis with very narrow leaves had stipules of the same width as the wide leaved plants. The variation in the stipules of the plants of C. bupleurifolia shown in Figure 5 represents the variation in a single population (2943) and is extreme for the Iocaulon Crotalarias. In some of the larger C. bupleurifolia plants observed in the field, the stipules were cupped as though the margins of the decurrent stipule had reached a maximum size before the stem had completed elongation.

Most of the Iocaulon Crotalarias grow in dry situations where moisture availability is sporadic. When drought conditions last for a long period of time the leaves may all be lost, but the stipules which wing the stem remain in good condition for a longer period. When moisture again becomes available, the photosynthetic tissue in the stipules may aid in the plant's recovery and give the stipule-bearing plants a survival advantage over non-stipule bearers under the same conditions. Crotalaria stipularia plants in this recuperating condition, with new shoots present, were described as the variety serpyllifolia by Senn (1939).

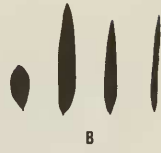
#### Leaves

Senn, in his 1939 treatment of Crotalaria, recognized varieties in C. sagittalis, C. pilosa, and C. stipularia based primarily on leaf size and shape. None of these varieties are recognized as being different from the typical varieties in this study.

Early leaves of all plants in the group tend to be round, oval, or elliptic with later leaves usually being narrower (Figure 6) except in plants with typically round or oval mature leaves (eg. Crotalaria rotundifolia). This leaf variation relative to the position on the stem was maintained under

---

Figure 6. Silhouettes of Crotalaria leaves from single plants with the lower leaves appearing on the left and the upper leaves on the right, .25x. A. C. rotundifolia var. rotundifolia (W&W 2385). B. C. sagittalis (W&W 2631). C. C. purshii (W&W 2660). D. C. stipularia (Howard 17,264). E. C. nayaritensis (W&W 2902). F. C. polyphylla (W&W 2859). G. C. quercetorum (W&W 2928).



greenhouse and growth chamber conditions where the temperature was moderated and moisture levels were maintained. The change of leaf shape from the base of a plant to the top is not uncommon and is especially noticeable in plants with lobed or dissected leaves. The pattern of leaf size reduction seems to be under genetic control and may relate to the efficiency of the vascular system at increasing distances from the roots.

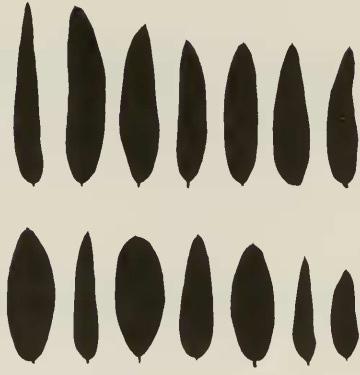
Because of the fact that the shape of leaves tends to vary with their position on the stem (Figure 6), the choice of leaves for comparison is problematic. The silhouettes in Figures 7 through 11 show representative leaf variation in field populations collected during this study. All leaves were taken from the upper half of the plants sampled, thereby avoiding most of the variation due to their position on the stem.

There is limited leaf shape variation in a given population of Crotalaria sagittalis, but variation between populations over the extensive range of the species is much greater. A comparison of the leaves represented in 7 B (Illinois) with 7 D (Louisiana) shows clearly the difference in leaf width which can be observed in northern and southern United States populations of this species. Every degree of variation between the two exists with the two figured samples approaching the extremes of a cline. The leaves of Mexican material of C. sagittalis (Figure 7 A) are more variable in shape than those of typical United States plants and may reflect a pool of variability in Mexico from which the United States C. sagittalis was derived.

Leaf variation in populations of Crotalaria rotundifolia var. vulgaris is quite limited in the United States and Mexico (Figure 8 A, B, C). Although the leaves from field collections from Mexico are larger than the United States material of the same variety, when planted together in the garden the differences in leaf sizes were not maintained. Leaves of C. rotundifolia var. rotundifolia are extremely variable in most populations,

---

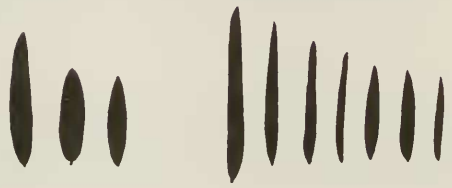
Figure 7. Silhouettes of Crotalaria sagittalis leaves showing variation in plants from different populations in different geographic areas, .25x. A. W&W 2996 (Veracruz). B. W&W 2777 (Illinois). C. W&W 2780 (Iowa). D. W&W 2631 (Louisiana).



A



B



C

D

Figure 8. Silhouettes of Crotalaria rotundifolia leaves showing variation in plants from different populations, .25x. A. var. vulgaris (W&W 2892, Nayarit). B. var. vulgaris (W&W 2900, Nayarit). C. var. vulgaris (W&W 2771, South Carolina). D. var. rotundifolia (W&W 2377, Florida). E. var. rotundifolia (W&W 2384, Florida). F. var. rotundifolia (W&W 2379, Florida).

Figure 9. Silhouettes of Crotalaria leaves showing variation in plants from different populations, .25x. A. C. purshii (W&W 2772, South Carolina). B. C. purshii (W&W 2684, Florida). C. C. purshii (W&W 2687, Florida). D. C. stipularia (Howard 17,264, Puerto Rico).

Figure 10. Silhouettes of Crotalaria leaves showing population variation in plants from different populations, .25x. A. C. bupleurifolia (W&W 2943, Jalisco). B. C. polyphylla (W&W 2860, Durango).

Figure 11. Silhouettes of Crotalaria leaves showing variation in plants from various populations, .25x. A. C. nayaritensis (W&W 2897, Nayarit). B. C. nayaritensis (W&W 2902, Nayarit). C. C. quercetorum (W&W 2928, Jalisco).

as might be expected in plants that are usually self-pollinated but which outcross occasionally.

Patterns of leaf variation in Crotalaria purshii are similar to those observed in United States plants of C. sagittalis, with broader leaves occurring on plants in the northern populations and narrow leaves occurring in the southern populations. Figure 9 A, from South Carolina plants of C. purshii, is representative of variation which can be observed in these plants from southern Virginia to northern Georgia, while Figure 9 B and C, from Florida material, are representative of leaf width of plants of C. purshii in the southern portion of its range.

While Figure 9 D illustrates only the variation included in a single population of Crotalaria stipularia, sufficient variation is shown to place some of the plants into Senn's variety typica and others into his variety grandifolia. Senn's variety serpyllifolia has even smaller leaves than variety typica, but the specimens he cites are all plants in the process of recovering



A



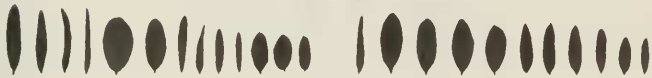
B



C



D



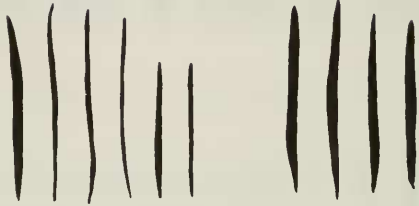
E

F

Figure 8



A



B

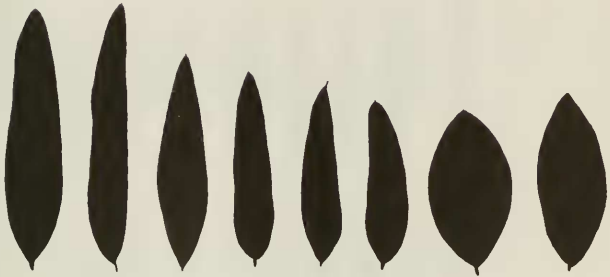
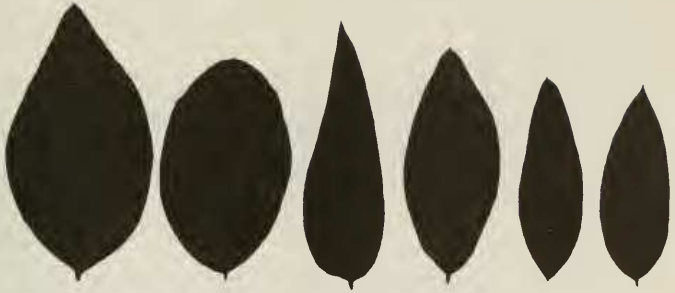
C



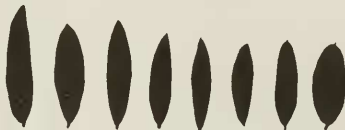
D

Figure 9





A

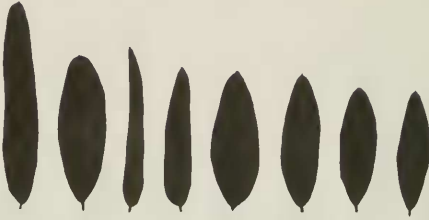


B

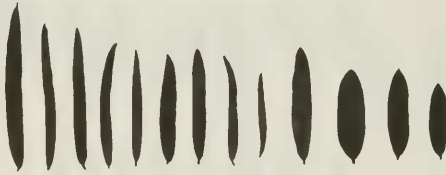
Figure 10



A



B



C

Figure 11

from drought conditions, as shown by the lack of leaves on the main stem.

Populations of Crotalaria bupleurifolia (Figure 10) show a great deal of plant to plant leaf variation similar to that seen in C. rotundifolia var. rotundifolia (Figure 8 D or E). Crotalaria polyphylla leaves resemble in shape and size those of C. rotundifolia which led Senn (1939) to include this group of plants in his C. maritima (here treated as C. rotundifolia var. rotundifolia).

Leaf variation in Crotalaria nayaritensis resembles that in C. bupleurifolia, but C. nayaritensis lacks the leaf size seen in C. bupleurifolia (Figure 11 A and B).

Crotalaria quercetorum leaves (Figure 11 C) resemble those of C. purshii in some instances, and C. quercetorum was recognized as a variety of C. purshii by Senn (1939) on this basis. Like C. purshii, C. quercetorum regularly has glabrous upper leaf surfaces.

Crotalaria plants growing in sunny conditions tend to bear leaves which are thicker and more succulent than leaves of plants growing in shaded conditions, even in the same populations. The leaf shapes observed in field plants of all species were maintained in their garden-grown progeny, although the size of leaves ultimately produced was slightly smaller.

#### Inflorescences and Bracts

Inflorescences in Iocaulon Crotalarias are lax-flowered racemes borne either terminally or opposite a leaf. The terminal position is probably the most primitive inflorescence position in the group, with inflorescences opposite a leaf being developed from it by reduction of the raceme and the development of the axillary bud between the raceme and the uppermost leaf. Each flower on the raceme is subtended by an elliptic or lanceolate bract which may be stalked or un-stalked. Bracts are also found on the peduncle below the lowest flower and may represent the locations of aborted flower buds. The shape and size of these lower bracts is usually similar to those subtending the flowers, but the bract number is not constant in a species. Bract characters have been considered by several authors to be diagnostic and have been used to distinguish varieties and species. For example,

Senn (1939) used bract type as an important character in separating Crotalaria tuerckheimii from C. sagittalis. Bracts and other characters used to segregate C. tuerckheimii are, however, too variable to warrant the recognition of the species. Fernald (1950) recognized a variety of C. purshii (C. purshii var. bracteolifera) based on a larger bract number, narrow leaves, and increased branching. Wilbur (1963) indicated that the variety showed no ecological separation and that it probably was no more than an extreme form. Examination of herbarium material of the variety and of collections made during this study leads me to agree with Wilbur.

#### Flowers

As mentioned above, flower structure has been used by Polhill (1968) to define sections in the genus Crotalaria. Polhill uses the pubescent bilabiate calyx which bears a bracteole near the base, the glabrous ovary, and the long, twisted keel to characterize section Calycinae. Figure 12 presents representative drawings of the floral parts in the Iocaulon species of Crotalaria.

#### Bracteoles

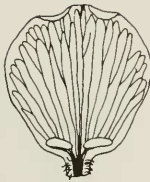
A pair of bracteoles is always present on the calyx of Iocaulon Crotalaris, with one located basally on each side. The bracteoles vary a great deal in size and shape from population to population and though the bracteoles are smaller than the bracts, variations in their size and shape are directly related. The bracteoles reach mature size earlier than the flower bud and are longer than the bud during the early stages of bud development, placing them in a protective position during bud development. Barneby (1964), in the introduction of his Atlas of North American Astragalus, indicates that bracteoles of similar structure and position in Astragalus are "very probably homologous to the stipules which they resemble in form". In Astragalus the similarity between the stipules and bracteoles is clear, but in the Iocaulon Crotalaris it is not evident.

---

Figure 12. Floral parts of Iocaulon Crotalaria flowers, 1.7x. A. Calyx, split on one side to show all lobes. B. Banner. C. Wing petal. D. Keel, showing twisting of the carina. E. Androecium. F. Gynoecium.



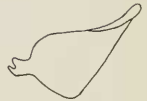
A



B



C



D



E



F

## Calyx

The calyx in the *Iocaulon Crotalaria*s consists of a short campanulate tube which bears five unequal lobes arranged in a bilabiate fashion. The calyx is foliaceous in texture and bears trichomes on the outside only. The two upper calyx lobes, which in the open flower are positioned behind the banner, are each about 1.5-2 times as wide as each of the lower three calyx lobes. Of the three lower calyx lobes the center lobe may be equal to or slightly narrower than the lateral lobes. The three lobes may be either coherent or free at the tips at anthesis. The calyx does not enlarge or becomes only slightly enlarged during fruit development and turns brown as the mature fruit changes from green to black. Figure 13 illustrates calyx size and form in the United States *Iocaulon Crotalaria* species. Variation in the calyces tends to be essentially random, but plants of species with an extensive north-south range have small calyces in the northern part of the range and large in the south.

## Corolla

The *Iocaulon Crotalaria* corolla is typically papilionaceous and is composed of an adaxial standard or banner, two free wings, and a keel which consists of two petals which are coherent at their margins and appear fused in the twisted portion of the carina. The banner is formed by a broad blade and a short pubescent claw. At the base of the blade and just above the claw are a pair of petaloid appendages (Figure 12 B). The wing petals consist of a blade and a twisted claw, with the claw attached laterally to the blade (Figure 12 C). The adaxial

---

Figure 13. Outlines of calyces from garden grown plants of *Crotalaria*, .87x. Each calyx has been cut along one side and flattened to show all five lobes. A. *C. purshii* (W&W 1190) North Carolina. B. *C. purshii* (W&W 2772) South Carolina. C. *C. purshii* (W&W 2704) Florida. D. *C. purshii* (W&W 2668) Mississippi. E. *C. sagittalis* (W&W 2777) Illinois. F. *C. sagittalis* (W&W 2846) Alabama. G. *C. sagittalis* (W&W 2848) South Carolina. H. *C. sagittalis* (W&W 2631) Louisiana. I. *C. rotundifolia* var. *rotundifolia* (W&W 2672) Mississippi. J. *C. rotundifolia* var. *rotundifolia* (W&W 2398) Florida. K. *C. rotundifolia* var. *rotundifolia* (W&W 2372) Florida. L. *C. rotundifolia* var. *vulgaris* (W&W 2768) South Carolina. M. *C. rotundifolia* var. *vulgaris* (W&W 2650) Louisiana.



A



B



C



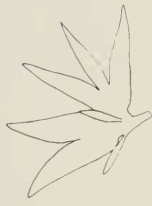
D



E



F



G



H



I



J



K



L



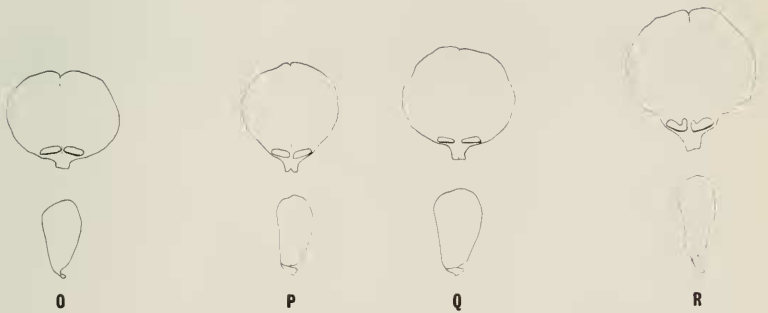
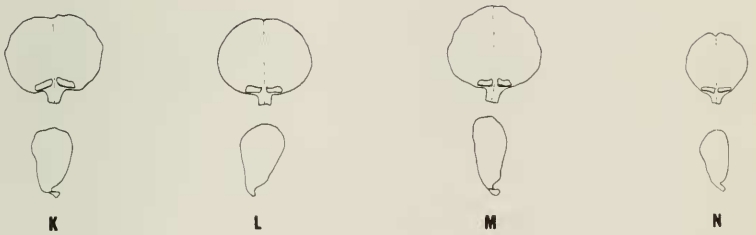
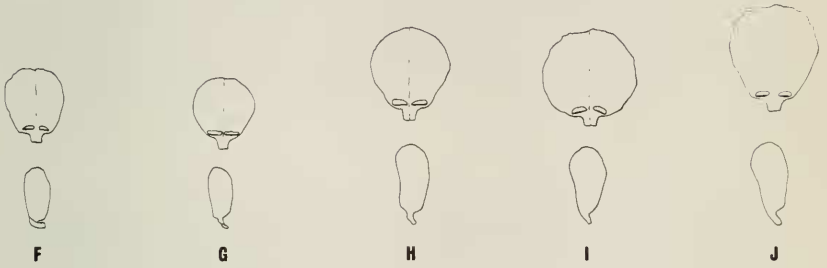
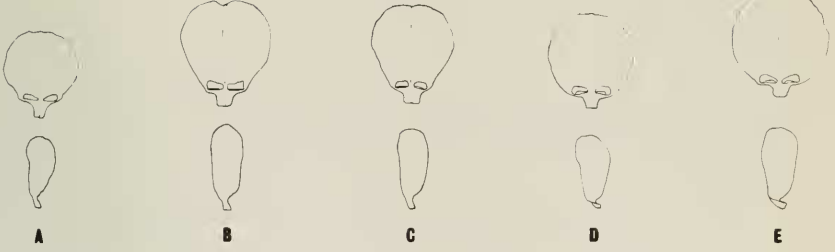
M

margins of the wing blades curve over the top of the keel and form the surface on which visiting insects land. Wing petals from collections of all species showed a puckering of the petal tissue between the veins, but no species-specific pattern of variation in the puckering is apparent. Representative banner and wing petals from United States plants of Crotalaria rotundifolia, C. sagittalis, and C. purshii are shown in Figure 14. A tendency, though not a clear cut one, toward a smaller petal size in the northern portions of the ranges of C. purshii and C. sagittalis and a larger one in the southern portions can be seen in the material illustrated in Figures 14 A-J. Petal size in C. rotundifolia var. rotundifolia (Figure 14 K-N) is very close to the petal sizes of C. purshii and C. sagittalis in the southern part of their ranges (Figure 14 C, D, F and H, I, J). Crotalaria rotundifolia var. vulgaris regularly tends to have a larger petal size than any of the other United States Iocaulon taxa regardless of latitude. As was indicated in the above section on pollination, available information seems to indicate that United States C. sagittalis may be self-pollinating. In the greenhouse, flowers of northern plants of C. sagittalis (W&W 2777) have been observed to set fruit without the banner ever being displayed in a position which might attract insects. Self-pollination may have made the display of a large and showy banner obsolete, but over most of the range of subsection Iocaulon reduced selection has not resulted in the reduction of the size of the showy banner. In the rather homogeneous northern annual populations there is a trend toward a smaller banner size. Although larger banner size is probably not detrimental to the plants

---

Figure 14. Outlines of banner and wing petals from garden grown plants of Iocaulon Crotalarias, .87x. A. C. purshii (W&W 1190) North Carolina. B. C. purshii (W&W 2772) South Carolina. C. C. purshii (W&W 2752) Georgia. D. C. purshii (W&W 2704) Florida. E. C. purshii (W&W 2668) Mississippi. F. C. sagittalis (W&W 2780) Iowa. G. C. sagittalis (W&W 2777) Illinois. H. C. sagittalis (W&W 2848) South Carolina. I. C. sagittalis (W&W 2846) Alabama. J. C. sagittalis (W&W 2631) Louisiana. K. C. rotundifolia var. rotundifolia (W&W 2351) Florida Keys. L. C. rotundifolia var. rotundifolia (W&W 2358) Florida. M. C. rotundifolia var. rotundifolia (W&W 2384) Florida. N. C. rotundifolia var. rotundifolia (W&W 2672) Mississippi. O. C. rotundifolia var. vulgaris (W&W 2768) South Carolina. P. C. rotundifolia var. vulgaris (W&W 2415) Florida. Q. C. rotundifolia var. vulgaris (W&W 2669) Mississippi. R. C. rotundifolia var. vulgaris (W&W 2650) Louisiana.





in the North, the alleles for large petal size may be closely associated with alleles for some other character which is selected against in the colder northern climates.

Although the keel, which encloses the androecium and gynoecium, varies in size from species to species, it is constant in shape and in all cases appears as seen in Figure 12 D. The claws of the keel petals are attached laterally at the base of the ovary.

Color of the banner and wings of the *Iocaulon* species is usually a bright yellow, but in some instances a population may have some plants which produce bright yellow petals and others with creamy white petals. Contrary to Polhill's (1968) description of section *Calycinae*, members of this subsection usually have banners which are lined with brown or purple along the veins near the base. The adaxial surface of the banner frequently becomes reddish in all species when exposed to sunlight. This reddish color may become purple or bluish when the plant is dried. The keel petals, which are usually covered by the wings, are white to greenish white.

#### Androecium and Gynoecium

The androecium of *Crotalaria* is monadelphous and is composed of ten stamens with alternating long basifixed and short medifixed, tetralocular anthers which dehisce by longitudinal slits. The staminal tube surrounds the lower half of the ovary and is split on the adaxial side (Figure 12 E).

The mature pistil is composed of a glabrous, cylindrical, elongate ovary bearing a style which is geniculate at the base (Figure 12 F). The style bears a spiral of trichomes and terminates in a trichome-bearing stigma.

During the early stages of bud development, the elongate anthers are well developed and lie in a ring around the pistil with the style being only slightly longer than the elongate-anthered stamens. The short anthers are slower in maturation than the elongate anthers and are positioned near the base of the elongate anthers in these stages. As the bud develops the style elongates and the stamen filaments begin to develop. Just prior to the opening of the bud, the short anthers are still positioned just below the elongate anthers, but as the filaments continue to elongate, the short anthers are elevated to a position

above the elongate anthers. In some flowers which have been examined, the short anthers are elevated to a point adjacent to the stigma, thus increasing the probability of self-pollination.

Polhill (1968) reported that in living Crotalaria plants which he observed, nectar was secreted from the receptacle at the base of the stipitate ovary. Although this has not been established for the small flowered Iocaulon plants, it is considered to be likely because of the behavior of visiting insects observed on the garden plants of the various species.

#### Pollen

Pollen grains of plants in subsection Iocaulon develop in a tetrahedral tetrad. The grains are triaperturate and sub-spheroidal when viewed with one of the poles exactly uppermost (ambit view), and the surface of the grains is unadorned. The pollen size range is 15.5-31.1 microns which places the pollen into the small and lower-medium size classes suggested by Erdtman (1952).

A survey of pollen size in the Iocaulon Crotalarias was undertaken using pollen from plants from the randomized garden plot. Fresh pollen was removed from the keel of one flower from each of two plants, mixed in glycerol jelly with acetocarmine, and observed at a magnification of 430x. All collection locations represented in the garden were sampled. One hundred stained grains were measured from each slide two to three hours after preparation. Unstained grains observed during the measuring were tallied to obtain a measure of pollen viability as shown by stainability (Owezarszak, 1952). All pollen samples were at least 90% stainable and most were better than 95% stainable. This high stainability was expected because of the regular meiotic behavior exhibited in the group. Table 7 presents the statistical analysis of the pollen samples and the stainability percentages.

The pollen size ranges of single species overlap to the extent that no species may be separated from the others on the basis of pollen grain diameter. The ranges of pollen size within a species are so broad that in species which are distributed over a large area the largest mean  $\pm 1$  SD. does not overlap with the smallest mean  $\pm 1$  SD. In some genera pollen size variation of this magnitude would indicate that several ploidy levels were present. Since all known chromosome counts in the

TABLE 7.

POLLEN SIZE (IN MICRONS) AND STAINABILITY FOR *Crotalaria* SPECIES.  
ALL FIGURES ARE BASED ON A SAMPLE SIZE OF 100 POLLEN GRAINS.

Species and Number	Country and State	Range	Mean	Standard Deviation	Standard Error	Pollen Stainability
<u><i>Crotalaria nayaritensis</i></u>						
2897	MEX, Nay.	15.48-21.93	19.13	0.97	0.097	100%
2902	MEX, Nay.	16.77-21.93	19.60	0.91	0.091	100%
<u><i>Crotalaria polyphylla</i></u>						
2849	MEX, Dur.	19.35-23.22	20.45	1.15	0.115	100%
2857	MEX, Dur.	19.35-24.51	21.32	1.12	0.112	98%
2860	MEX, Dur.	19.35-24.51	22.20	1.41	0.141	97%
<u><i>Crotalaria purshii</i></u>						
1190	US, N.C.	20.64-25.80	23.01	1.11	0.111	100%
2668	US, Miss.	20.64-25.80	22.96	1.26	0.126	100%
2704	US, Fla.	18.06-21.93	19.25	0.83	0.083	99%
2752	US, S.C.	20.64-27.09	23.54	1.60	0.160	96%
2772	US, S.C.	19.35-24.50	22.01	1.29	0.129	97%
<u><i>Crotalaria quercetorum</i></u>						
2917	MEX, Nay.	19.35-24.51	21.78	1.28	0.128	100%
2928	MEX, Jal.	20.64-27.09	24.45	1.44	0.144	97%

TABLE 7. (Continued)

Species and Number	Country and State	Range	Mean	Standard Deviation	Standard Error	Pollen Stainability
<u>Crotalaria rotundifolia</u> var. <u>rotundifolia</u>						
2358	US, Fla.	18.1-24.5	20.96	1.28	0.128	100%
2366	US, Fla.	18.1-24.5	21.30	1.32	0.132	99%
2367	US, Fla.	16.8-27.1	21.67	1.70	0.170	98%
2372	US, Fla.	19.4-25.8	21.67	1.37	0.137	92%
2375	US, Fla.	18.1-23.2	20.73	1.20	0.120	100%
2377	US, Fla.	15.5-19.4	18.47	1.07	0.107	94%
2384	US, Fla.	19.4-25.8	21.39	1.55	0.155	92%
2398	US, Fla.	19.4-24.5	22.19	1.26	0.126	100%
2421	US, Fla.	16.8-24.5	20.34	1.60	0.160	96%
2672	US, Miss.	19.4-23.2	20.20	1.86	0.186	98%
2756	US, Ga.	18.1-21.9	20.02	1.12	0.112	94%
Stimson 2096	US, Fla.	19.4-23.2	21.07	1.15	0.115	100%
<u>Crotalaria rotundifolia</u> var. <u>vulgaris</u>						
2411	US, Fla.	18.1-23.2	20.09	0.98	0.098	99%
2415	US, Fla.	20.6-25.8	23.71	1.32	0.132	99%
2645	US, La.	19.4-25.8	23.25	2.06	0.206	94%
2650	US, La.	19.4-24.5	21.17	1.26	0.126	100%
2669	US, Miss.	19.4-25.8	23.57	1.34	0.134	99%
2706	US, Fla.	18.1-20.6	19.47	0.76	0.076	96%

TABLE 7. (Continued)

Species and Number	Country and State	Range	Mean	Standard Deviation	Standard Error	Pollen Stainability
2718	US, Fla.	19.4-25.8	23.34	1.15	0.115	100%
2730	US, Fla.	19.4-25.8	22.99	1.78	0.178	100%
2762	US, Ga.	19.4-24.5	21.80	1.17	0.117	98%
2768	US, S.C.	18.1-21.9	19.50	1.12	0.112	98%
2900	MEX, Nay.	18.1-23.2	19.80	0.01	0.001	100%
2952	MEX, Jal.	20.6-25.8	23.66	1.29	0.129	98%
3017	MEX, Gua.	18.1-23.2	21.12	1.78	0.178	95%
3035	MEX, Mor.	19.4-25.8	23.62	1.50	0.150	95%
<i>Crotalaria sagittalis</i>						
2631	US, Ia.	16.8-21.9	19.23	1.16	0.116	100%
2777	US, Ill.	19.4-25.8	22.46	1.57	0.157	94%
2780	US, Iowa	18.1-21.9	19.81	1.01	0.101	90%
2846	US, Ala.	20.6-25.8	23.53	1.51	0.151	99%
2848	US, S.C.	19.3-24.5	21.22	1.39	0.139	97%
2891	MEX, Nay.	19.4-23.2	21.00	1.02	0.102	98%
2944	MEX, Jal.	19.4-27.1	22.90	2.00	0.200	93%
2950	MEX, Jal.	20.6-24.5	22.29	1.17	0.117	99%
2954	MEX, Jal.	16.8-24.5	20.39	1.64	0.164	98%
2966	MEX, Mich.	21.9-31.0	25.90	2.08	0.208	100%
2961	MEX, Mich.	20.6-27.1	24.54	1.81	0.181	100%
2968	MEX, Mich.	19.4-24.5	21.93	1.55	0.155	98%

TABLE 7. (Continued)

Species and Number	Country and State	Range	Mean	Standard Deviation	Standard Error	Pollen Stainability
2981	MEX, Oax.	18.1-21.9	19.80	0.74	0.074	99%
2996	MEX, Vera.	20.6-25.8	23.74	1.31	0.131	98%
<u>Crotalaria stipularia</u>						
Irwin 1050	Guyana	20.6-27.1	23.79	1.58	0.158	98%
Stimson 4264	Puerto Rico	18.1-25.8	21.97	1.40	0.140	97%

Iocaulon *Crotalaria*s are the same ( $n=16$ ), ploidy level cannot be used to explain the variation. The fact that all of the pollen parents were growing under relatively constant garden conditions when the pollen was sampled would lead to the conclusion that the pollen size differences observed are primarily genetically controlled rather than due to different environmental conditions. That pollen size does not correlate well with climate is evidenced in the United States material of *Crotalaria sagittalis* when a northern Illinois collection (W&W 2777) from about the same climate as a collection from Iowa (W&W 2780) had a mean pollen size of  $22.45\mu$  compared with a mean of  $19.81\mu$  for the Iowa population. In *C. purshii* a collection from North Carolina (W&W 1190) had a mean pollen size of  $23.01\mu$  which was almost identical with the mean of  $22.96\mu$  of W&W 2668 from southern Mississippi. Until such time as a clear relationship can be established between pollen size and some other character it may be assumed that selection for pollen size is random within the pollen size limits of the Iocaulon *Crotalaria*s.

#### Fruits

Fruits of *Crotalaria* plants are inflated pods which are sessile or short-stipitate. The pods of some plants are nearly cylindrical, but more frequently the tips of the pods have a larger circumference than the bases (Figure 15). Seeds are borne in two rows, one on each side of the adaxial suture of the pod. As the fruit matures and dries, the pericarp becomes black and the seeds within break loose. When the pod is moved a rattling sound is produced which prompts the use of the common name "rattle box" for members of the group.

Primary dispersal in *Crotalaria* fruits is a type of autochory which van der Pijl (1969) places under the category of an "active ballist", a common type in the Leguminosae. The first sign of impending dehiscence is the separation of the two valves along the center part of the adaxial suture. Continued

---

Figure 15. Photographs of fruits of *Crotalaria* species, ca. .55x. A. *C. sagittalis* (W&W 2777, United States). B. *C. rotundifolia* var. *vulgaris* (W&W 2730, United States). C. *C. rotundifolia* var. *rotundifolia* (W&W 2366, United States). D. *C. sagittalis* (W&W 2968, Mexico). E. *C. polyphylla* (W&W 2857, Mexico). F. *C. quercetorum* (W&W 2928, Mexico). G. *C. stipularia* (Stimson 4264, Puerto Rico). H. Putative hybrid between *C. sagittalis* and *C. rotundifolia* (W&W 2712, United States).





drying results in the further separation of the suture and the explosive inward and upward movement of the lower suture causing the dispersal of the seeds within. The valves continue to curl up in the same direction, frequently trapping a few seeds in each of the curled valves.

The distance to which seeds are thrown by the explosive action of the valves has not been determined for Crotalaria field material, but in the laboratory seeds have been thrown for distances up to about 5 meters. Ridley (1930) repeats reports of legume seeds being thrown by such torsion dehiscence in Lupinus digitatus for distances of 7 meters and in Bauhinia purpurea, a small tree, for distances as long as 12 meters. Regardless of the distance a seed is thrown, such dehiscence probably does not represent the major dispersal mechanism in Crotalaria. Movement of the individual seeds by water and animals probably accounts for most dispersal through the large territory where Crotalaria has become naturalized.

Since Crotalaria fruits dehisce readily when dried, only rarely are any mature fruits present with herbarium specimens. The large number of plants growing in the garden provided an excellent opportunity to gather data on the number of fruits per plant, number of seeds per fruit, and fruit size. In field collections most plants had fewer than ten fruits present at the time of a visit. In the experimental garden, 19 plants of C. sagittalis produced an average of 231 fruits per plant; far in excess of the number produced by single plants in their native habitats. Peduncles in the garden plants were no longer and bore no more flowers than those of their seed parents, but due to larger plant size the number of peduncles was greatly increased.

A summary of data on fruit size, number of fruits per plant, and number of seeds per fruit for garden grown Crotalarias is presented in Table 8.

The large plants of Crotalaria nayaritensis produced only a few fruits in the garden which reflects the fact that very few flowers were produced by the plants during the growing season. As mentioned earlier, this may have been due to unfavorable photoperiod conditions for bud formation. On the other hand, plants of C. polyphylla, which also had a very small average number of fruits per plant, flowered profusely in the garden.

TABLE 8.  
 DATA ON FRUIT NUMBER PER PLANT, SEEDS PER POD AND FRUIT SIZE IN GARDEN GROWN Crotalaria PLANTS.

Species and Country	Number of Samples	Total Number Plants	Fruits per Plant	Number Fruits in Seed Counts	Seed Number per Fruit	Number Fruits Measured	Fruit Length (mm)	Fruit Width (mm)
<u>C. nayaritensis</u> -Mexico	2	41	0.3-0.5	7	4-38	7	13-20	4.5-8.0
<u>C. polyphylla</u> -Mexico	3	49	0.8-9.2	15	2-12	33	11-22	4.0-8.0
<u>C. purshii</u> -U. S.	5	96	4.0-8.6	138	2-42	225	0-31	3.0-12.5
<u>C. quercetorum</u> -Mexico	2	38	8.5-122.5	238	4-52	182	0	4.0-11.0
<u>C. rotundifolia</u> var. <u>rotundifolia</u> -U. S.	13	234	5.7-55.0	997	1-57	912	12-42	4.0-12.5
<u>C. rotundifolia</u> var. <u>vulgaris</u> -U.S.	10	166	27.5-42.9	858	3-53	790	13-31	5.0-13.0
<u>C. rotundifolia</u> var. <u>vulgaris</u> -Mexico	4	74	22.8-136.2	439	2-68	426	7.5-29	3.0-12.0
<u>C. sagittalis</u> -U.S.	5	82	91.2-231.0	568	2-35	498	11-35	5.0-19.0
<u>C. sagittalis</u> -Mexico	11	209	1.9-144.9	1,989	2-67	1,006	8-33	3.0-16.0
<u>C. stipularia</u> -Puerto Rico	2	38	34.3-131.7	88	14-68	42	20-34	7.0-11.0

In this case the low fruit number may have been caused by a failure of the plant to self-pollinate at this latitude or an absence of its usual pollinator. Plants of C. quercetorum, a close relative of the Mexican C. sagittalis, grew to a larger size and were more densely branched than their field parents, as were plants of C. sagittalis. This increase in overall size is reflected in the large number of fruits per plant. Plants of C. purshii and C. rotundifolia only attained a garden size similar to that found in their field parents and consequently fruit production in these garden plants was more nearly like that found in field plants. Plants of some populations of C. rotundifolia var. rotundifolia from habitats with soils high in calcium did not grow well in the more acid soils of the botanical garden and consequently produced fewer fruits.

In an effort to get some figures for seed production potential in a single plant, the average seed number per fruit was multiplied by the average fruit number per plant for each sample. The range of potential seed production was great with nine samples having an average of under 100 seeds per plant and 14 samples with averages over 2,000 seeds per plant. Two of the samples (W&W 2996 and Stimson 4264) had averages of over 5,000 seeds per plant. Although these numbers were produced in conditions which are rare in the field, they do give a picture of what can happen when competition is reduced and sufficient water and nutrients are available for more nearly optimum growth.

Such variation is shown in seed number per fruit and fruit size that no diagnostic value in these characteristics was detected, nor were any clear patterns revealed when the data were compared with geographical distribution. As mentioned above, fruit number per plant is related to plant size and although some species apparently have low total production potential, this is not useful for diagnostic purposes since a single field plant would only bear a portion of its potential at once and not all of the fruits produced would be present at collection time.

#### SPECIES RELATIONSHIPS

The current center of distribution of the genus Crotalaria is in Africa where the genus is represented by about 400 species.

Section Calycinae, however, reaches its maximum diversity in Asia where it is represented by some 50 species: substantially more than the ten species of the section on the African continent. Polhill (1968) suggests that the New World species are of later origin, arriving via eastern Asia. His appraisal seems accurate inasmuch as a number of the Indian species (including C. alata and C. prostrata) are morphologically similar to the American species.

It would be interesting to obtain complete information on breeding systems and chromosome numbers in the Asian and African Calycinae species of Crotalaria. These plants have the typical papilionaceous corolla which evolved in response to insect selection, and may be self-sterile over much of their Old World range. The New World species, on the other hand, are mostly self-compatible. Outside the New World all species of the genus for which chromosome counts are available have been reported as  $n=8$ , while reports for the American species of Calycinae are all  $n=16$ . It is possible that the development of polyploidy in the genus was coincident with the evolution of self-fertility in the genus, both probably occurring at the time of dispersal to the New World. Following dispersal, when only a single seed might germinate in a habitat, the plant would have to be self-compatible for further seed to be produced. This would result in strong selection for self-compatibility. Since polyploidy frequently tends to reduce self-incompatibility it is possible that the same regime which was selective for self-compatibility would also be selective, indirectly, for polyploidy in the genus.

Baker (1955) linked "long distance" dispersal with the establishment of self-fertilization and Stebbins (1957) cites several examples of genera which are regularly cross-fertilized in their Eurasian distribution centers and chiefly self-fertilized in greatly disjunct peripheral areas like the Americas (Bromus, Secale, Primula, Armeria, Limonium). Available information would suggest that Crotalaria may well belong in this group, but until more information on breeding systems and chromosome numbers in the Asian species becomes available no sure assessment can be made.

Assessing relationships in a genus in which the breeding system appears to vary between self- and cross-fertilization is at best difficult, especially when many of the populations are

isolated in mountainous areas allowing individual populations to become more or less morphologically distinct from other populations. When data on cross-compatibility, chromosome morphology, and chromosome pairing are not available, speculation on the phylogeny in a group is limited to the author's appraisal of morphological characters as he has observed them in laboratory, garden, and field studies. When examining the proposed relationships set forth below it must be kept clearly in mind that the relationships suggested are considered by the author to best fit the currently available information; with further study other interpretations of the data may be possible and may prove to be more accurate.

The diagram of probable relationships presented (Figure 16) attempts to relate the species and varieties without indicating a direct linear relationship between extant species. All are shown as radiating from a common ancestral stock and are placed on common radii with closely related species. Major factors which have been used to construct the diagram include current distribution as well as morphological characters.

The prototypes of the subsection probably became established in southern Mexico and Central America and spread from these areas. The probable characteristics of such a prototype would likely have been the following:

1. Habit and Duration--caulescent perennials with taproots and one to several erect or ascending stems.
2. Stipules--foliaceous, decurrent stipules. Since the New World members of section Calycinae are thought to have originated from Asian stock which also have a similar type of stipule, it is probable that the ancestral plants which migrated to the New World also had such stipules causing separate evolution of the decurrent stipules in this hemisphere to be improbable. It should be pointed out that while ancestral forms of the North American Iocaulon Crotalarias probably had stipules, presence or absence of stipules in modern forms is considered to be neither primitive nor advanced, but merely evidence of several evolutionary pathways.
3. Leaves--broad, oval to round leaves. There seems to be a trend in most of the New World Iocaulon species for young plants to have broad early leaves and

narrower later leaves. There also seems to be a tendency for plants in moist habitats to have broad leaves and those in more rigorous, dry open habitats to have narrow ones.

4. Inflorescences--terminal. The terminal inflorescence position is a primitive type from which the leaf-opposed position could easily have evolved. Activation of the bud in the axil of the upper-most leaf at the base of a terminal inflorescence would give a leaf-opposed and lateral position to the inflorescence.

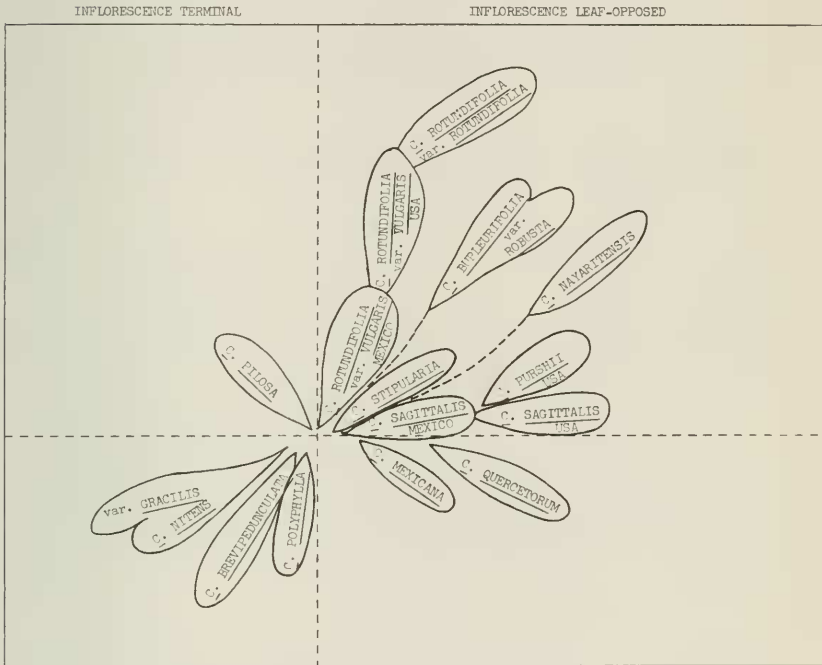


Figure 16. Possible relationships in North American Iocalon *Crotalariae Calycinae*.

5. Flowers--flowers are very similar throughout the group and except for size most species are so variable that one cannot be separated from the other on the basis of flower characters. Ancestral types were probably somewhat variable in size, but similar to our present species in over all structure.
6. Fruits--fruits in the *Iocaulon* species are very much alike in general form and any prototype would be expected to have had a similar fruit. The dull black coloration which is characteristic of fruits of plants in this subsection would also be present in the prototype plants. (The distribution of the black colored fruit in other sections is not known, but specimens of a number of other species of other sections observed in fruit lack it.)

As may be seen from Figure 16, most of the North American species are those with leaf-opposed inflorescences and with stipules present. The exact relationships between these species are obscured by the extreme variation present within them.

The group of species with terminal inflorescences and stipules present is represented in North and Central America only by *Crotalaria pilosa*, a species which ranges into South America where other similar species occur. The two species, *C. mexicana* and *C. quercetorum*, which lack stipules and have leaf-opposed inflorescences appear to be related to *C. sagittalis* from Mexico and Central America, but are quite distinct from it and from each other.

Three species lack stipules and have terminal inflorescences. Of these *C. nitens* has a distribution which extends into South America where other closely related species grow. The remaining two species, *C. brevipedunculata* and *C. polyphylla*, are plants of north and western Mexico which have quite limited distributions and differ from *C. nitens* in habit, general flower size, and peduncle length.

#### LITERATURE CITED

Baker, H.

1955. Self-compatibility and establishment after "long-distance" dispersal. *Evolution*, 9:347-348.

Barneby, R.

1964. Atlas of North American Astragalus. Printed as Vol. 13 of the Memoirs of the New York Botanical Garden. 1,188 pages. New York.



- Britton, W.  
1903. Vegetation of the North Haven Sand Plains. Bulletin of the Torrey Botanical Club, 30:571-640.
- Conklin, M.  
1936. Studies of the root nodule organisms of certain wild Legumes. Soil Science, 41:167-185.
- Cook, M.  
1924. Development of seed of Crotalaria sagittalis. Botanical Gazette, 77:440-445.
- Corner, E.  
1951. The leguminous seed. Phytomorphology, 1:117-150.
- Erdtman, G.  
1952. Pollen Morphology and Plant Taxonomy. Angiosperms. 539 pages. Waltham, Massachusetts.  
1954. An Introduction to Pollen Analysis. 239 pages. Waltham, Massachusetts.
- Kempanna, C. and K. Sastry.  
1958. Male sterility in Crotalaria striata. Current Science, 27:181.
- Kingsbury, J.  
1964. Poisonous Plants of the United States and Canada. 626 pages. Englewood Cliffs.
- Maerz, A. and M. Paul.  
1950. A Dictionary of Color. Edition 2. 208 pages. New York.
- Martin, R. and C. Cushwa.  
1966. Effects of heat and moisture on Leguminous seed. Tall Timbers Fire Ecology Conference. Proceedings, 5:159-175.
- Merrill, E.  
1949. Index Rafinesquianus. 296 pages. Jamaica Plain.
- Metcalf, C. and L. Chalk.  
1950. Anatomy of the Dicotyledons. 2 volumes. Oxford.
- Miller, R.  
1967. Crotalaria Seed Morphology, Anatomy and Identification. USDA Technical Bulletin #1373. 73 pages. Washington, D. C.
- Owczarzak, A.  
1952. A rapid method for mounting pollen grains, with special regard to sterility studies. Stain Technology, 27:249-51.
- Pijl, L. van der.  
1969. Principles of Dispersal in Higher Plants. 153 pages. Berlin-Heidelberg.
- Polhill, R.  
1968. Miscellaneous notes on African species of Crotalaria L.: II. Kew Bulletin, 22:169-348.
- Quick, C.  
1961. How long can a seed remain alive? in Seeds, 1961 Yearbook of Agriculture. 591 pages. Washington, D. C.

Rafinesque-Schmaltz, C.

1836. New Flora and Botany of North America. 4 parts. Philadelphia.

Ridley, H.

1930. The Dispersal of Plants Throughout the World. 744 pages. Ashford.

Senn, H.

1939. The North American species of Crotalaria. Rhodora, 41:317-366.

Stebbins, G.

1957. Self-fertilization and population variability in the higher plants. The American Naturalist, 91:337-354.

Wilson, J.

1944. The nodulating performance of three species of Legumes. Proceedings Soil Science Society of America, 9:95-97.

Windler, D. R.

1970. Systematic Studies in Crotalaria sagittalis L. and related species. Unpublished dissertation, University of North Carolina at Chapel Hill.

1971. New North American unifoliolate Crotalaria taxa (Leguminosae). Phytologia. 21:257-266.

Wodehouse, R. P.

1935. Pollen Grains. 574 pages. New York.